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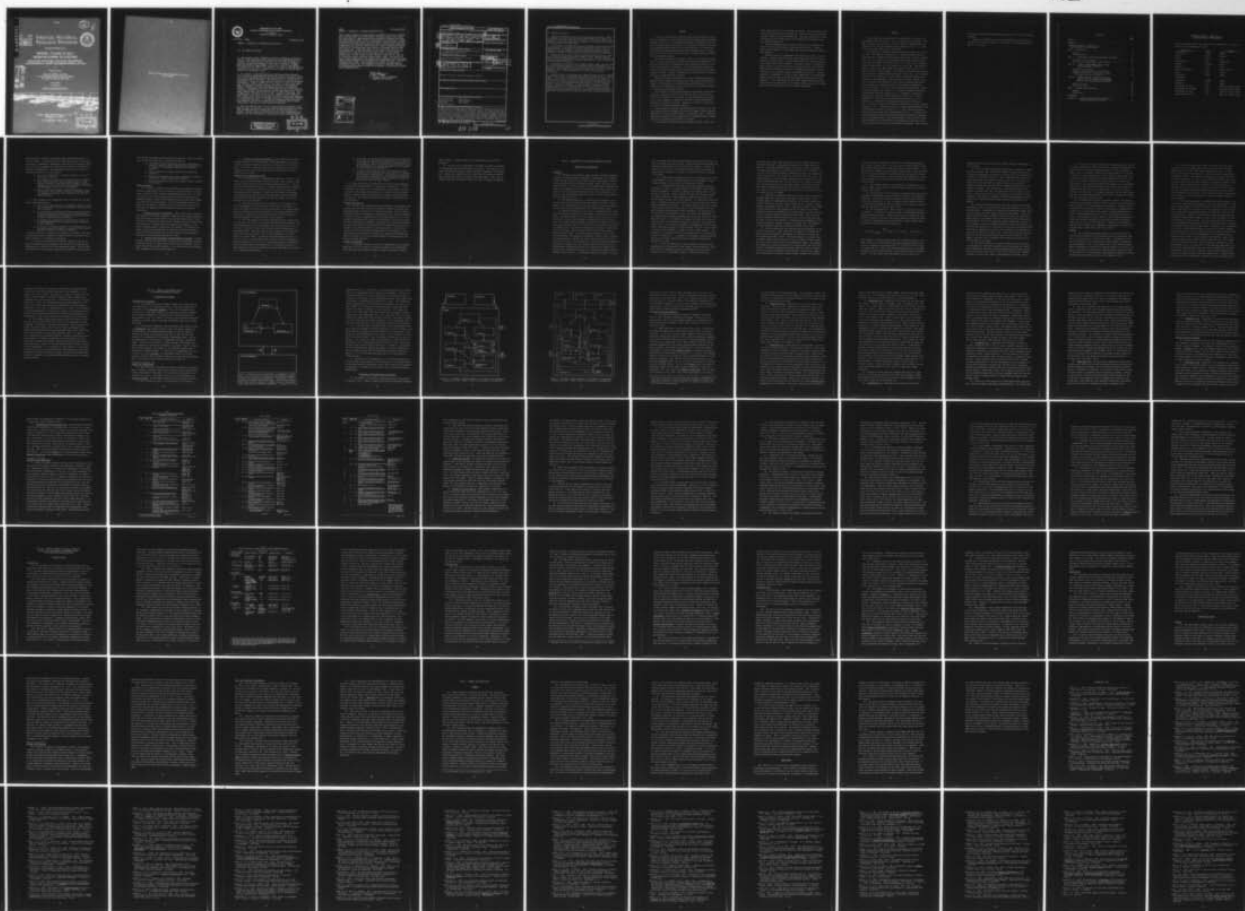   JAN 78 D GUNNISON
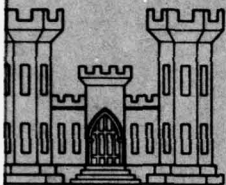UNCLASSIFIED   WES-TR-D-78-3   NL

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DREDGED MATERIAL
RESEARCH PROGRAM

TECHNICAL REPORT D-78-3

MINERAL CYCLING IN SALT
MARSH-ESTUARINE ECOSYSTEMS

ECOSYSTEM STRUCTURE, FUNCTION, AND GENERAL
COMPARTMENTAL MODEL DESCRIBING MINERAL CYCLES
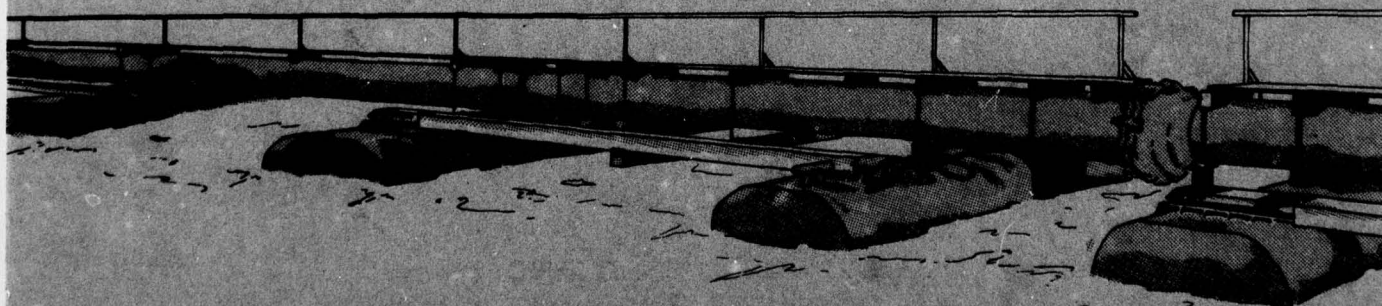
by

Douglas Gunnison

Environmental Effects Laboratory
U. S. Army Engineer Waterways Experiment Station
P. O. Box 631, Vicksburg, Miss. 39180

January 1978
Final Report

Approved For Public Release; Distribution Unlimited

Prepared for Office, Chief of Engineers, U. S. Army
Washington, D. C. 20314

Under DMRP Work Unit No. 2A05

DEPARTMENT OF THE ARMY

WATERWAYS EXPERIMENT STATION, CORPS OF ENGINEERS

P. O. BOX 631

VICKSBURG, MISSISSIPPI 39180

IN REPLY REFER TO: WESYV   15 February 1978

SUBJECT: Transmittal of Technical Report D-78-3

TO: All Report Recipients

1. The technical report transmitted herewith represents the results of
Work Unit 2A05 regarding mineral cycling in salt marsh-estuarine eco-
systems. This work unit was conducted as part of Task 2A (Effects of
Marsh and Terrestrial Disposal) of the Corps of Engineers' Dredged
Material Research Program (DMRP). Task 2A is a part of the Habitat
Development Project (HDP) of the DMRP and is concerned with defining and
quantifying the effects of dredged material disposal on shallow water,
wetland, and terrestrial sites.

2. The purpose of this work unit was to address nutrient and heavy
metal cycling in marsh-estuarine ecosystems through an intensive litera-
ture survey, discussions with recognized authorities, and application of
information from allied fields. The specific area of concern was the
environmental impact of dredged material disposal in marsh and estuarine
environments. A major conclusion of this report is that present knowl-
edge is inadequate to permit accurate predictions of environmental
impacts resulting from marsh development with heavily contaminated
material. Consequently the author recommends that only those materials
containing nutrients and heavy metals in no greater amount than those in
nearby natural marsh soils should be used for marsh development. This
recommendation is justified at this time. However, several DMRP work
units (4A06, 4A11H, 4A11L, 4A15A, 4A26, introduced below) have specifi-
cally addressed the potential hazards involved in shallow-water disposal
of contaminated materials. A preliminary assessment of the resultant
data indicates that accurate quantification techniques will be forth-
coming with a synthesis of this research information.

3. Work Unit 2A05 was one of several research efforts designed by the
DMRP to assess the potential for the uptake and mobilization of contami-
nants through disposal of dredged material in marsh and estuarine
systems. Closely related work units were 4A06, which demonstrated the
effect of Eh, pH, and salinity on heavy metal uptake by marsh plants;

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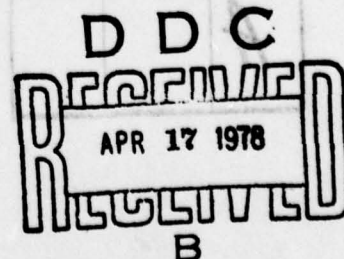
4A11H, which compared the water quality and sediment status of a natural
and a man-made marsh on the James River, Virginia; 4A11L, which evalu-
ated the uptake of organohalides from contaminated sediments into plant
and animal tissues; 4A15, in which marsh plants were subjected to various
concentrations of heavy metals in a hydroponic solution; 4A15A, in which
an extraction procedure was developed to predict heavy metal uptake from
dredged material; and 4A26, which provided a rapid, inexpensive bioassay
technique for predicting heavy metal uptake from dredged material under
field conditions. Additional supportive and comparative data will be
forthcoming with the final analysis of the results of field studies at
Windmill Point, Virginia (4A11); Buttermilk Sound, Georgia (4A12);
Apalachicola, Florida (4A19); Bolivar Peninsula, Texas (4A13); Pond No.
3, California (4A18); and Miller Sands, Oregon (4B05). The results of
these research products will be integrated in a synthesis report entitled
"Upland and Wetland Habitat Development with Dredged Material: Ecological
Considerations" (2A08). That document will provide the Corps with a
comprehensive basis for sound management decisions regarding disposal
in marsh-estuarine systems and habitat development on potentially contami-
nated dredged material.

JOHN L. CANNON
Colonel, Corps of Engineers
Commander and Director

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Dredged material	Mineral cycling
Ecosystems	Salt marshes
Estuarine ecology	

20. ABSTRACT (Continue on reverse side if necessary and identify by block number)

A nutrient and heavy metal cycling study of marsh-estuarine ecosystems was undertaken for the Dredged Material Research Program. The study objective was to gather as much of the existing information as possible on mineral cycling in marsh-estuarine ecosystems. A compartmental model outlining pathways of mineral cycling within the marsh-estuarine ecosystem was developed. Approaches used in the study included literature surveys and discussions with authorities in marsh-estuarine ecology. Information from allied fields of research was used to supplement direct sources of information. (Continued)

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20.   ABSTRACT (Continued).

Marshes and estuaries function as a single integrated ecosystem. Marshes are dependent on estuaries for their origin and maintenance, and supply 50 to 95 percent of the total organic matter contained in the estuarine water column. Detritus of marsh origin forms the major portion of a food chain that supports an extensive estuarine-based fishery.

The proximity of oxidizing and reducing environments within marsh-estuarine ecosystems permits the nitrogen and sulfur biogeochemical cycles to exist in complete forms. The intimacy of oxidizing-reducing zones permits oxidation of ammonium to nitrate, followed by anaerobic production of molecular nitrogen. Reduction of sulfate to sulfur and sulfide also requires anaerobic conditions.

Marsh-estuarine ecosystems regulate phosphorus release to the sea. Marsh grasses mobilize phosphorus by acting as pumps, steadily removing phosphorus from soil and then losing phosphorus to estuarine water. Estuarine regenerative processes remove phosphorus from decomposing marsh grasses. Some of this phosphorus also moves to the ocean.

Heavy metals, including dissolved inorganic cadmium, copper, and lead, move out to sea through the estuary. The particulate forms of these metals are deposited within the ecosystem along with insoluble compounds formed from iron and manganese. Zinc and mercury move through the system, but are slowed in their passage because of their involvement with estuarine biota and organic particulates.

Chemical release of contaminants from dredged materials may cause problems. Oxygen demands exerted by reduced materials placed in aerobic waters can deplete oxygen. Several heavy metals have increased mobility once their binding sulfides have been oxidized. Oxidation of heavily contaminated marsh soils can cause metal toxicity for plants and cat clay formation. Eutrophication resulting from use of contaminated materials for marsh creation is not a problem, except in unproductive estuaries. Present knowledge is inadequate to permit accurate predictions of environmental impacts resulting from use of heavily contaminated materials in marsh creation. It is recommended that only those dredged materials containing nutrients and heavy metals in quantities no greater than those in marsh soils at the creation site be used for marsh development.

SUMMARY

A nutrient and heavy metal cycling study of marsh-estuarine ecosystems was undertaken for the Dredged Material Research Program to address problems concerning: (a) environmental impacts of dredged material disposal in marsh-estuarine ecosystems, (b) pollution of estuaries from use of contaminated dredged materials for marsh creation, (c) heavy metal mobilization by marsh primary producers and subsequent metal concentration in the biota, and (d) harmful effects of dredged material disposal on marsh-estuarine ecology.

The study objective was to gather as much of the existing information as possible on mineral cycling in marsh-estuarine ecosystems; this was used to construct a compartmental model outlining pathways of mineral cycling within the ecosystem. The study approaches included an intensive literature survey and discussions with authorities in marsh-estuarine ecology. Indirect information from allied fields of research was used to supplement direct sources.

Marshes and estuaries function as a single integrated ecosystem. Marshes, while dependent on estuaries for their origin and maintenance, supply 50 to 95 percent of the total organic matter contained in the estuarine water column; this forms the base of a food chain supporting an extensive estuarine-based fishery.

The proximity of oxidizing and reducing environments within marsh-estuarine ecosystems permits the nitrogen and sulfur biogeochemical cycles to be completed. The intimacy of oxidizing-reducing zones permits aerobic oxidation of ammonium to nitrate, followed by anaerobic production of molecular nitrogen. Reduction of sulfate to sulfur and sulfide also requires anaerobic conditions.

Marsh-estuarine ecosystems regulate phosphorus release to the sea. Marsh grasses mobilize phosphorus by acting as pumps, steadily removing phosphorus from soil and then losing it to estuarine water. Estuarine regeneration processes remove phosphorus from decomposing marsh grasses. Some of this phosphorus then moves to the ocean.

Heavy metals, including dissolved inorganic cadmium, copper, and

lead, move easily out to sea through the estuary. The particulate forms
of these metals are deposited within the ecosystem along with insoluble
compounds formed from iron and manganese. Zinc and mercury move through
the system but are slowed because of involvement with estuarine biota
and organic particulates.

Present technology does not give a viable means of assessing the
exact or even a general value of each unit area of marsh. However,
destruction of marshes is environmentally unsound and should be avoided
when possible.

Chemical release of contaminants from dredged materials can cause
problems. Oxygen demand exerted by reduced materials placed in aerobic
waters may deplete oxygen. Several heavy metals have increased mobility
once binding sulfides are oxidized. Oxidation of heavily contaminated
marsh soils can cause metal toxicity for plants and cat clay formation.
Eutrophication resulting from use of contaminated materials for marsh
creation is not a problem, except in unproductive estuaries. Present
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ing nutrients and heavy metals in no amounts greater than those in marsh
soils at the creation site be used for marsh development.

PREFACE

This research was supported by the Dredged Material Research Program (DMRP), Work Unit 2A05, of the U. S. Army Corps of Engineers. The DMRP is sponsored by the Office, Chief of Engineers (DAEN-CWO-M), and administered by the Environmental Effects Laboratory (EEL), U. S. Army Engineer Waterways Experiment Station (WES).

The research was conducted during the period November 1974 to October 1975. The study was conducted by Dr. Douglas Gunnison, Research Microbiologist, Ecosystem Modeling Branch, EEL, under the direct supervision of Dr. R. L. Eley, Chief, Ecosystem Research and Simulation Division, EEL, and general supervision of Mr. D. L. Robey, Chief, Ecosystem Modeling Branch, EEL. Dr. John Harrison was Chief, EEL. The study was funded as part of the DMRP Habitat Development Project with Dr. H. K. Smith serving as Project Manager. Many persons provided valuable assistance during the information-gathering phase of the study. The staff and students of the University of Georgia Marine Institute, Sapelo Island, Georgia, and the Department of Agronomy and the Coastal Studies Institute, Louisiana State University, Baton Rouge, Louisiana, were particularly helpful in providing literature and technical information. Dr. W. H. Allaway, U. S. Plant, Soil, and Nutrition Laboratory, Cornell University, Ithaca, New York; Dr. W. M. Dunstan, Skidaway Institute of Oceanography, Savannah, Georgia; Dr. J. L. Gallagher, University of Georgia Marine Institute, Sapelo Island, Georgia; Dr. S. P. Meyers, Department of Food Science, Louisiana State University; Dr. W. H. Patrick, Jr., Department of Agronomy, Louisiana State University, Dr. L. R. Pomeroy, Department of Geology, University of Georgia, Athens, Georgia; Dr. R. J. Reimold, University of Georgia Marine Resources Extension Program, Brunswick, Georgia; Dr. J. W. Teal, Woods Hole Oceanographic Institute, Woods Hole, Massachusetts; and Dr. I. Valiella, Boston Marine Program, Marine Biological Laboratory, Woods Hole, Massachusetts, contributed much of their valuable time in providing the principal investigator with background on marsh-estuarine ecosystems and on various aspects of mineral cycling in aquatic ecosystems. Many of these

persons also kindly provided detailed descriptions of their own research programs.

Directors of WES during the study and preparation of this report were COL G. H. Hilt, CE, and COL J. L. Cannon, CE. Technical Director was Mr. F. R. Brown.

CONTENTS

CONVERSION FACTORS: METRIC TO U. S.
EQUIVALENT UNITS OF MEASUREMENT

Metric (SI) units used in this report can be converted to U. S. customary units of measurement as follows:

Multiply	By	To Obtain
centimetres	0.3937	inches
litres	0.264	gallons
metres	3.281	feet
square metres	10.76	square feet
microns	0.00004	inches
hectares	2.471	acres
square centimetres	0.155	square inches
grams	28.35	ounces
milligrams	0.028	ounces
micrometres		
millimetres	0.0394	inches
kilograms	0.454	pounds
micrograms per gram	1.00	parts per million (ppm)
milligrams per kilogram	1.00	parts per million (ppm)
milligrams per litre	1.00	parts per million (ppm)
micrograms per litre	1.00	parts per billion (ppb)

MINERAL CYCLING IN SALT MARSH-ESTUARINE ECOSYSTEMS

ECOSYSTEM STRUCTURE, FUNCTION, AND GENERAL
COMPARTMENTAL MODEL DESCRIBING MINERAL CYCLES

PART I: INTRODUCTION

Problem

1. As a result of the passage of the River and Harbor Act of 1970
(Public Law 91-611), the Corps of Engineers was authorized to initiate
an extensive environmental research program on dredged material disposal.
In a subsequent study by the U. S. Army Engineer Waterways Experiment
Station (WES) (Boyd et al., 1972), one of the possible productive uses
contemplated for dredged material was as a source of new marsh substrate
for the creation of additional salt marsh habitat.

2. During the process of artificial salt marsh establishment,
several potential difficulties may be encountered, including the achieve-
ment of proper substrate elevations for marsh plant development, the
selection of marsh species that are compatible with the environmental
conditions at the site, and the successful dissemination and establish-
ment of marsh plant propagules in the new marsh. Hopefully, several on-
going studies being conducted as part of the Dredged Material Research
Program (DMRP) will provide adequate guidance to solve these potential
problems. However, a field office conducting a marsh development pro-
ject or any other activity involving the movement or disposal of dredged
material in marshes and estuaries always must answer a question that
poses problems of even greater magnitude: What will be the environ-
mental impacts of dredged material disposal in the salt marsh-estuarine
ecosystem? The National Environmental Policy Act of 1969 (Public Law
91-190) and the Federal Water Pollution Control Act Amendments of 1972
require an evaluation of the potential environmental impacts of proposed
management activities in an ecosystem prior to the initiation of such
work.

3. Coastal wetlands in general and marsh-estuarine ecosystems in particular require close examination to assess the potential effects of dredged material disposal within these environments. Marsh-estuarine ecosystems are biologically and economically important to man and to nature. Their high productivity and consequent importance is partially a result of the close biogeochemical and physical coupling between marshes and estuaries. The coupling, as will be described later, is intense enough to warrant consideration of salt marshes and estuaries as one ecosystem. Therefore, perturbations in a marsh have potential effects on the ecology of the estuary and vice versa (Teal, 1962; Pomeroy et al., 1972; Gosselink et al., 1973; and Eley et al., 1975a). For example, if the dredged material used for marsh development were contaminated, would the new marsh be a source of contamination for the surrounding estuaries? If the dredged material contained excessive levels of plant nutrients, would the developing marsh be overproductive and, perhaps, be responsible for the eutrophication of adjacent estuaries? In addition, if the dredged material were contaminated with high concentrations of heavy metals, could these metals be mobilized by some biogeochemical mechanisms with the subsequent concentration of such contaminants in the salt marsh-estuarine food web? Also, dredging and dredged material disposal in estuaries might have significant and harmful consequences on the ecology of marshes or might serve to decrease the total area of productive marshes at a given site.

4. Several projects have been initiated by the DMRP to assess the impact of artificial marsh creation, and several reports on this subject have been prepared (Barko et al., 1977; Eley et al., 1975a; and Lee et al., 1976). However, the ability to effectively address the problem of Corps activities in the marsh-estuarine ecosystem has been somewhat hampered by the failure to have available all current information on nutrient and heavy metal cycling in thse coastal ecosystems.

Study Objectives

5. The major purpose of this study was to gather as much of the currently existing information on nutrient and heavy metal cycling in

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marsh-estuarine ecosystems as possible under existing constraints of time and money. In order to make this knowledge available in an easily used form, a diagrammatic compartmental model was to be formulated that would outline the pathways of mineral cycling within the ecosystem and between its compartments. The compartmental model had the following constraints placed on its construction:

a. It was to be developed in a detail reflective of the current state of the art.

b. The format was to consist of a generalized set of compartments (marsh substrate, detritus, marsh grasses, decomposers, herbivores, carnivores, water, plankton, benthos, sediment, etc.); for each of these compartments, a detailed subcompartmental model was to be formulated.

c. The data obtained on mineral cycling, specifying the rate, form, amount, and direction of transfer of minerals among the components, were then to be integrated into the compartmental model.

6. The information thus summarized would be available to the DMRP for the following purposes:

a. To serve in guiding work unit experimental studies by pointing out areas where pertinent environmental information was weak or lacking.

b. To provide Corps of Engineers District and Division offices concerned with coastal activities with a factual body of available information on the mineral cycling and associated ecology of marsh-estuarine ecosystems.

c. To emphasize the implications of these mineral cycles to the environmental effects of dredged material disposal in coastal ecosystems.

d. To serve as a reference document for the preparation of environmental impact statements in conjunction with Corps of Engineers activities in coastal ecosystems.

In addition, the data on mineral cycling would be available to any persons desiring general information on marsh-estuarine ecosystems for research purposes or for mathematical modeling.

7. In order to effectively integrate all aspects of mineral cycling in marsh-estuarine ecosystems, a second parcel of knowledge was assembled and incorporated into the compartmental model. This information consists of the biological, chemical, and physical entities, which

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collectively characterize marsh-estuarine ecosystems. Thus, this report will provide the reader with a general knowledge of:

    a. The important major biological, chemical, and physical processes operating within marsh-estuarine ecosystems and the names of the organisms, materials, or processes involved.

    b. Several important ecological functions of marshes and estuaries.

    c. Some of the predominant biological, chemical, and physical interactions between marshes and estuaries.

    d. Some of the possible origins and potential fates of marshes and estuaries.

Study Approaches

8. To provide information on the structure and function of marsh-estuarine ecosystems as well as on mineral cycling within these ecosystems, a series of three separate study approaches were used. In order to ensure that the facts obtained were both current and accurate, an attempt was made to obtain corroborating evidence for the same information with each of the approaches. The following methods were used to gather the information: intensive survey of literature, contact with authorities in marsh-estuarine ecology, and recourse to indirect information.

9. Intensive survey of literature. Many current journal articles were surveyed in the areas concerned. Books were used where appropriate. The work of Teal and Teal (1969) on the salt marsh and Perkin's (1974) treatise on estuarine and coastal water biology were particularly useful starting points. Pertinent articles supplied by authorities in the field of marsh-estuarine ecology were also helpful. In addition, the normal literature survey methods of examining literature obtained by cross-reference from journal and review articles and backtracking of references from abstracting journals were used.

10. Contact with authorities in marsh-estuarine ecology. Personal contacts were made and discussions held with known authorities in marsh-estuarine ecology or closely allied fields either by telephone, at pertinent regional and national meetings, or by on-site visits with authorities conducting relevant ongoing research.

11. <u>Recourse to indirect information.</u> When information was unobtainable directly from the literature or from appropriate authorities, indirect information obtained from other relevant areas of research was used. The fields of agronomy, plant ecology, aquatic and soil microbiology, plant-soil chemistry, and fisheries biology were especially useful sources of data.

Formulation of compartmental model

12. The development of a compartmental model was a process of continual evolution and refinement during the entire study. However, three distinct stages occurred during the model formulation process. An initial model formulated by Eley et al. (1975b) served both as the starting point for the literature search and as the prototype from which succeeding models were developed. In addition, this model also provided the organizational structure upon which particular details concerning marsh-estuarine biology, chemistry, ecology, and physics could be assembled as they were obtained.

13. The general model, which is described in this report, is a direct descendant of the initial model of Eley et al. and differs in only a few important details from the initial model. The general model serves to integrate the major compartments of the marsh-estuarine ecosystem into a descriptive diagram that outlines the major pathways or potential pathways of mineral cycling in the ecosystem.

14. The final stage in the model development was the construction of rate tables for each of the nutrients and heavy metals examined. The rate tables present data on the amount, form, and direction as well as the rate of transfer of each of the minerals between compartments of the general model. Each rate table has been related to the appropriate part of the model by numbers of the various compartments or arrows within the general model. In addition, relationships between each of the tables and its corresponding model component have been explored in depth by discussions in the text. A nutrient-by-nutrient and metal-by-metal accounting system was selected over the alternative process of going through all nutrients and metals for each compartment of the model on an individual bases because:

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a. It provides the greatest continuity within a given mineral's cycle; that is, one nutrient or metal and all the facets of its movement through the ecosystem have been presented in a single package. Thus, its cycling may be traced easily and any ramifications of ecosystem perturbation to the cycling of this mineral can be understood.

   b. It enables one nutrient or metal to be studied in detail separate from the clouding that could exist if all minerals were discussed simultaneously. This permits a person who is interested in only one or two of the minerals presented here to get the information without having to separate the desired facts from all other details.

15. While this method of presentation does have these advantages, the method necessarily entails a large degree of repetition. To avoid overwhelming the reader who is interested only in the general patterns of mineral cycling while providing access to details for the research worker, a special approach has been used to separate general knowledge from details. The differences between the packages of information are as given below.

Contents of main text

16. The main text presents general descriptions of salt marshes and estuaries and describes in detail the manner in which the general compartmental model is related to the natural ecosystem. Once the general model itself has been presented, a description of the types of organisms or abiotic entities occupying each of the compartments is given. A description is presented for each of the interactions listed as occurring between compartments in the model. Following this, general descriptions are made of the cycling of each nutrient or heavy metal; these are then related to the patterns evident in the general model. Data are presented in the text for mineral cycling within the constraints of the general model and from this, conclusions are drawn and recommendations made with respect to the use of marsh-estuarine ecosystems for the disposal of dredged materials.

Contents of appendix

17. The appendix focuses on each of the compartments in the general model and, in turn, presents the detailed contents of the compartment. Each individual table, then, presents a study of a nutrient or heavy

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metal cycling to a depth reflective of the present state-of-the-art knowledge.

18. The main text is intended for use where the details contained in the appendix may be neither needed nor desired. The appendix is intended for general reference, impact statement preparation, and research use. However, the appendix does not repeat the more general ecosystem level descriptions, which are given in the main volume. Thus, the researcher will wish to review the main text before studying the appendix.

PART II: DESCRIPTION OF THE MARSH-ESTUARINE ECOSYSTEM

Overview of the Ecosystem

Estuaries

19. Estuaries are transition zones (ecotones) between freshwater
streams or rivers and marine ecosystems. Functionally, the estuary is
a body of water semi-enclosed by land in which fresh water of terres-
trial origin meets with and dilutes seawater (Odum, 1959; Reid, 1961;
Perkins, 1974). Since the estuary has a unidirectional freshwater cur-
rent in its headward end and an oscillating saline tidal system at its
mouth, the estuary necessarily possesses some of the properties and
biota of each contributing ecosystem as well as several characteristics
that are uniquely its own.

20. The dominant properties of the physical environment of the
estuary that can be characterized include sediment transport, morpho-
metry of the estuarine basin, mixing and salinity, color and turbidity,
current flow, heat, and temperature (Reid, 1961; Perkins, 1974).

21. Sediment transport has two facets. Sediments moved by fresh
water are imported through the erosive powers of streams in their water-
sheds. Following transport into the estuary, dense particles are de-
posited as a result of the decrease in transporting stream velocity
which occurs when incoming saltwater currents meet outgoing fresh water;
less dense particles fall out as a result of the coagulating activities
of saltwater ions. The result of depositional influences combined with
estuarine currents, tides, and wave actions are the construction of
deltas and tidal flats. After the erosive activities of waves have
scoured materials from headlands, peninsulas, offshore dunes, sandbars,
and bottom deposits, sediment can also be transported back into the
estuary from the sea. If inflowing salt water has sufficient magnitude,
materials are imported into the estuary from the sea (reverse flow).
Alternatively, suspended sediments may be imported by incoming tides
providing the incoming tidal current is sufficiently stronger that the
outgoing stream currents. For materials imported by seawater to build

up in an estuary, the import of materials must obviously exceed the export by outgoing tides and currents. Both stream and tidal deposits can contribute substantially to the filling of the estuary. Filling, in concert with the erosion of coastline features and in the absence of compensational uplifting or sinking of a region, can cause the demise of an estuary.

22. Estuarine basin morphometry can play a determining role in the establishment or lack of salinity gradients, the development of sedimentary features, and the degree of fluctuation of tides.

23. Although mixing and salinity are interrelated in estuarine ecosystems, salinity is a physicochemical factor rather than a purely physical phenomenon. Salinity is, perhaps, the dominant factor in the estuarine ecosystem. Because salinity increases the density of water, the lighter fresh water flows seaward through the estuary over the inland-flowing, denser, more saline seawater. As fresh water flows seaward, it gradually becomes more saline as a result of diffusive or turbulent exchanges with seawater. By contrast, because salt water becomes increasingly diluted with fresh water as it moves landward, the seawater becomes indistinguishable from fresh water. The amount and rate of this mixing are dependent not only on diffusion and turbulence at the saltwater and freshwater boundary, but also on the strength of winds and tides; these, if of sufficient strength, can hold back or even reverse the flow of the freshwater stream at flood tide. The pattern of outward flow in the estuary is dependent on morphometry of the estuary basin, direction and height of tides and winds, Coriolis' forces, degree of stratification (thermal or saline), and the current velocity. The magnitude of freshwater inflow into the estuary will also influence the pattern of outward flow. In general, the freshwater stream has greater influence on estuary composition during the heavier precipitation seasons (Reid, 1961).

24. Color and turbidity are often produced by dissolved humic substances and by suspended silt and organic detritus particles. These often impart a brownish appearance to estuarine waters that can be aerially visible for many miles seaward. Excessive turbidity in

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estuaries often causes light extinction at such a shallow depth as to make light limiting to phytoplankton growth and to bottom floral production. Heavy phytoplankton blooms can themselves impart coloration to waters, particularly in estuaries having little or no turbidity. In the case of more turbid estuaries, phytoplankton blooms may reach significant levels within a few centimeters of the surface of the water. In turbid estuaries, a zone of higher turbidity may be flanked on both the upstream and downstream sides by zones in which the turbidity decreases with increasing distance from the central region of greater turbidity. Such zones (turbidity maxima) oscillate upstream and downstream with each respective flood and ebb tide and may persist for prolonged periods in a given section of estuary.

25. There are two important aspects of current flow in estuaries: flushing number and tidal prism volume (Reid, 1961; Perkins, 1974). Flushing number is a mathematical description of the time required for a parcel of water to move out of the estuary and is, therefore, a measurement of discharge (Perkins, 1974). Tidal prism volume is that amount of water imported into the estuary from the sea during a flood tide. Knowledge of these two parameters plus stream inflow will give some idea of water exchange dynamics occurring in the estuary. The forces that actually generate estuarine currents are tides, stream flow, and wind. Th impact of these forces depends on estuarine basin morphometry, stream channel morphometry, seasonal variation in stream flow, tidal height, and tidal movement along with related wind effects (Reid, 1961).

26. Heat and temperature are additional physical parameters of importance in estuaries. Heat content may be imparted to estuarine water directly by solar radiation (insolation) or indirectly by stream and tidal additions (Perkins, 1974). The thermal regime in estuarine water is greatly affected by the depth of the sea into which the water enters, the tides, and the stability of the intruding salt wedge. The temperature regime also reflects fluctuations in thermal input from the stream source; a spring-fed stream would probably have less effect on temperature than a stream possessing a large watershed. More general temperature determinants of estuaries include climate, adjacent sea currents,

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and the seasonal periodicity of flooding of the marshes and mudflats (Reid, 1961; Perkins, 1974). The latter can be strongly warmed by summer sunshine but also may be severely cooled by winter climates. Estuarine vertical temperature distributions reflect depth, stream and tidal flow, and seasonal variation in latitudinal and longitudinal distribution. In temperate climates, temperature may vary seasonally in a pattern analogous to that occurring in dimictic lakes (Hutchinson, 1957; Perkins, 1974).

27. The chemical entities that dominate in estuarine waters include: oxygen, carbon dioxide, dissolved organic matter, pH, salinity, and dissolved solids.

28. Dissolved gases are influenced in estuarine waters by salinity, temperature, turbulence, current biological properties, and dissolved materials. The current biological properties and dissolved materials in estuarine waters are, in turn, determined by the chemical contents of the stream and seawaters and the position in the estuary of the gradient between these two waters (Nash, 1947).

29. The concentration of carbon dioxide is primarily influenced by salinity. An increase in salinity causes a corresponding decrease in carbon dioxide solubility. Solubility decreases with increasing temperature. However, salt water does have a chemical feature that tends to favor the solubilization of carbon dioxide. Carbon dioxide reacts with water in accordance with the equation:

$$CO_2 \rightleftarrows CO_{2\ aqueous} \overset{+H_2O}{\rightleftarrows} H_2CO_3 \rightleftarrows H^+ + HCO_3^- \rightleftarrows H^+ + CO_3^=$$
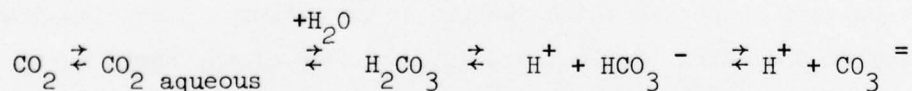
This equation is strongly pushed toward the bicarbonate (HCO_3^-) - carbonate ($CO_3^=$) side by the alkaline nature of seawater arising from an excess of cations of strong bases (Na^+, K^+, and Ca^{++}) over the anions of strong acids (Cl^-, $SO_4^=$, $PO_4^\equiv$) [618 milliequivalents of cations/kg of seawater vs 609 milliequivalents of anions/kg of seawater (Perkins, 1974)]. For this reason, the total amount of CO_2 in solution in

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estuarine waters will increase in the seaward direction, regardless of other factors.

30. There are many relationships between the occurrences of oxygen and carbon dioxide. The solubility of oxygen if greatly affected by salinity and temperature, an increase of either causes the concentration of oxygen in solution to decrease. Since temperature and salinity undergo both diurnal and seasonal variations, the levels of oxygen and carbon dioxide in the water are likewise subject to such shifts. Changes in oxygen and carbon dioxide are primarily biological and thus opposite in pattern. This difference is accentuated by the lack of reaction of oxygen with water in a manner that can be shifted by alkalinity. Bottom flora can use CO_2 and produce O_2 if not shaded out by turbidity. The presence or absence of salinity and temperature stratification also affects dissolved oxygen content at the bottom of the estuary.

31. Dissolved organic matter can enter the estuary from streams, groundwater, and, to a lesser extent, rain water (Valiela et al., report in preparation). Alternatively, dissolved and particulate organic materials can enter from local sources including tidal marshes. Dissolved organic materials consist largely of humic acids that have their primary origins in the marshes, but some fraction may also be generated in the watershed. Most of the particulate organic particles occurring in turbid estuaries consist of organic detritus of tidal marsh origin; such particles may comprise up to 90 percent of total seston (living and dead particulates suspended in the water) in an estuary in the immediate vicinity of the marsh (de la Cruz, 1973). Much of the humic matter transported to the estuary by incoming streams in acidic in nature. The humates often will tend to coagulate and precipitate upon meeting the cations found in salt water.

32. The pH of seawater, in contrast to that of most fresh water, is remarkably well buffered and tends to resist pH changes as a result of the presence of the carbon dioxide-carbonate buffer system, and the boric acid borate buffer system. This tends to restrict the saltwater pH range to 7.8-8.4 with a mean of approximately 8.2 (Harvey, 1955).

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33. The dissolved salts contributed to estuarine waters by the sea are nearly constant as a result of the sea's relatively homogeneous complement of major dissolved components relative to that of estuaries (Hoar, 1966). By contrast, fresh water can vary widely in its content of dissolved solids, although river waters generally contain more sulfate than chloride and more calcium than magnesium (Ross, 1970). This reason is, in itself, sufficient to permit estuaries to differ from each other in their chemistries without consideration of the tremendous variations in flow rate and dissolved solids content that a given inflowing stream may undergo on an annual basis. Since the estuarine salt water is diluted by its freshwater component, the dissolved solids can vary in concentration along the length of the estuary, with concentration increasing towards the mouth.

34. The amount and direction of movement of water, the salinity, temperature, and chemical factors are each critical to the organisms and have an impact on their distribution and well-being. Estuarine organisms must either be widely tolerant of fluctuations in temperature and salinity or else have adapted some means of confining themselves to a single, fairly homogeneous parcel of water that oscillates with the tides. The estuarine biota must adapt to a wide range and magnitude of diurnal and seasonal variations in salinity and dissolved chemicals rather than to a set of mean conditions. Tolerance to alterations in salinity with an emphasis on osmoregulatory adaptation is probably the most important response (Reid, 1961; Hoar, 1966).

Marshes

35. The salt marsh ecosystem develops on flat areas of mud or sand, which are sheltered from strong wave action by sand dunes, sand bars, or other barriers, or along river banks. An elevation of the physical substrate at or slightly above midtide height is optimal for marsh development. Such a flat elevation may result from the submergence or emergence of a section of coastline relative to sea level, the physical activities of winds, tides, and waves upon a section of land, or the deposition of mud and sand by the estuarine sedimentary processes previously described (Teal and Teal, 1969; Ranwell, 1972).

36. Once the substrate has reached the proper elevation, propagules from one of the marsh plant species that prefer the shoreline habitat can move in and, under proper conditions, develop. As many marsh grasses mature, they send out rhizomes from which separate plant populations develop. The presence of vegetation presents an obstacle to the tidal excursions. As a result, the currents in incoming tides can be slowed sufficiently to cause deposition of suspended sediments (Teal and Teal, 1969; Ranwell, 1972). In addition, organic materials are added to the marsh surface in the form of dead grass roots and rhizomes plus any decomposing aboveground vegetation that has not been scoured from the marsh by tide and storm. Thus, the marsh surface develops from its initial mud or sand composition to a mixture of muds or sands and plant residues.

37. With continued addition of sediments and plant materials, the level of the marsh surface can actually rise above mean midtide. If the rate of marsh growth is sufficient to permit the surface level to reach that of mean high tide, the marsh will then be flooded by only one half of the tides while being exposed during the other half. This lack of flooding causes a decrease in tidal sediment input, decreases the rate of growth in marsh surface height, and also limits the amount of nutrients available to marsh grasses. Once the marsh surface has risen to a level approximately 30 cm, about the level of mean high tide, an equilibrium between marsh growth and tidal input is achieved. As a consequence of the lack of tidal sediment input, the presence of poorer substrate-stabilizing grasses, and a decreased rate of plant matter accretion that shifts the marsh soil from an accumulating to a decomposing economy, the marsh level ceases to rise as rapidly (Teal and Teal, 1969). Continued decomposition of organic matter coupled with marsh soil compaction and erosion of marsh soil can cause an actual subsidence in the marsh surface level. Once the level of the marsh has been lowered to a point where marsh-building grasses can become reestablished, the level of the marsh can rise again. Normally, however, marsh building continues in a seaward direction from the original site. A large estuary may be formed at the confluence of several rivers and streams with the

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central estuary's salt wedge intruding along the bottoms of many or all of the component streams (as, for example, in Chesapeake Bay); in this case, each stream may possess a gradation of marsh types ranging from brackish marsh at the point of main estuary entrance to freshwater marsh farther upstream. The formation of pools in the marsh surface and the destruction of sections of marsh by storms or by submergence and elevation may proceed at rates in excess of the marsh's adjustment ability. However, the marsh surface is normally maintained at slightly above mean tide level by the elevating and depressing forces of tides, erosion, plant growth, compaction, and decomposition of peat (Teal and Teal, 1969; Ranwell, 1972).

38. Salt marshes are irrigated and drained by a series of channels that connect directly to the main body of the estuary. The channel system is, in fact, a part of the estuary and the component channels are termed tidal streams or creeks. Once developed in the marshes, these creeks may undergo changes in position similar to other rivers, including formation of oxbows, meandering, etc. Since the amount of water necessary to flood the marsh cannot be moved in channels of lesser capacity, the outgoing (ebb) tides are able to erode from the creeks any filling resulting from collapsing creek banks or deposition by the incoming (flood) tides (Teal and Teal, 1969; Chabreck, 1972).

39. The biota of the marshes are attuned to the periodic inundations by the tidal waters. In addition, the vegetative composition of the marsh itself is determined to some extent by the salinity of the flooding waters as well as the properties of the marsh soil (Chabreck, 1972). In a riverine estuary, the type of marsh on its borders will vary in a continuous gradation from a true salt marsh near the mouth of the estuary through brackish marshes at midestuary to freshwater marsh at the headwaters of the estuary (Reid, 1961). Similar gradations in marsh type may also be seen along tidal creeks with freshwater sources at their headwaters.

Interactions Between Marshes and Estuaries

40. Salt marshes and estuaries are closely coupled, and many

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interactions occur between them. As previously discussed, estuaries are
the sources of various physical and chemical substrates necessary for
marsh formation and development. The addition of nutrients to the marsh
either in the form of nutrient-laden sediments deposited on the marsh
surface or in the case of nutrient-poor sandy soils, in the form of nu-
trient-rich tidal waters, is a mechanism of plant fertilization.

41. Estuaries also support various herbivorous, detritivorous, and
carnivorous organisms that move up into the marsh with the flooding
tides in order to feed. In this manner, estuarine species are quite
dependent upon marsh production.

42. The destructive power of waves and shifting currents in estu-
aries can tear up the same marshes that have been built up by estuarine-
marsh interactive processes. In addition, the erosive power of rainfall
on the marsh at low tide can tear at the banks of tidal creeks, pro-
moting headward erosion of their tributaries, thus causing a further
dissection of the marsh surface with channels (Teal and Teal, 1969).

43. The processes of nutrient uptake from the sediments and scrub-
bing of nutrients from tidal waters enable marshes to store and subse-
quently to regulate the re-release of some of the nutrients to the estu-
ary in the form of particulate organic matter (especially carbon and
nitrogen). The dominant mechanisms of nutrient release from a marsh
include uptake of marsh soil nutrients by marsh grasses through their
root systems followed by release of some of these nutrients to water
through excretion from stems or leaves of living marsh plants and
through microbial decompostion of dead plant and animal materials.

44. Apparently marshes are important as a source of nutrition for
those estuarine animals that feed upon organic detritus (although some
authors feel otherwise; see Heinle and Farmer, 1976). The marshes are
the principal source of detritus to the estuaries. The continuous input
of large quantities of detritus permits estuaries to serve as nursery
grounds for large numbers of species of animals, many of which are
prized as sources of food or sport by man (Schelske and Odum, 1961; de
la Cruz, 1973).

45. In many ways, salt marshes act as buffers for estuaries. By

regulating the release of nutrients to the estuaries, marshes provide a
steady input level that minimizes periods of slack production in the
estuary (de la Cruz, 1973). By serving as a source of detritus for the
estuary, marshes enable the estuary to support trophic pathways that
supplement many estuaries that have a light-limited low level of primary
production. Indeed, the maximum detritus supply made available to the
estuary often occurs during the winter months when estuarine primary
production is at or near its minimum (Day et al., 1973). By functioning
as tortuous passageways for water during periods of localized heavy ter-
restrial runoff, marshes can decrease or ameliorate the suddenness with
which slugs of local runoff materials are discharged into the estuary.

46. The intimate relationship between marsh and estuarine ecosys-
tems has several implications with respect to the importance of these
ecosystems to terrestrial and marine environments. Marsh-estuarine eco-
systems are buffer zones on which marine storms may dissipate their
energies before moving inland and through which terrestrial runoff must
move before flowing out to sea (Teal and Teal, 1969). In addition,
these ecosystems are exceedingly important to marine ecosystems and to a
lesser degree to freshwater ecosystems as nursery grounds for biota.
Many marine organisms and several freshwater species use highly produc-
tive estuaries as a source of food and shelter during at least a portion
of their development. As a consequence of these functions, any of man's
activities that result in the destruction, contamination, or other per-
turbation of the marsh-estuarine ecosystem can have far-reaching effects
on marine, freshwater, and marsh-estuarine productivity and, ultimately,
upon man himself.

PART III: GENERAL COMPARTMENTAL MODEL
OF THE MARSH-ESTUARINE ECOSYSTEM

Structure of the Model

Organization of the model

47. The diagram persented in Figure 1 depicts the format used in
the construction of the compartmental model. The major subdivisions of
the model are the ecosystem components. These are the elements that
either form or exert major influences on the marsh-estuarine ecosystem.
The ecosystem components are contained within the blocks denoted by
Roman numerals I and II in Figure 1 and by the name "Ecosystem Component"
appearing in boldface type in the upper left-hand corner of each compo-
nent block.

48. The Ecosystem Component I block surrounds three smaller blocks
or compartments that contain the major biotic and abiotic elements of
this ecosystem. Although Ecosystem Component II could be similarly
divided, the detail is unnecessary here; this is also the case with
several of the components in the general compartmental model. Each of
the compartments is identified by a compartment name and a compartment
number. The latter is composed of a Roman numeral, which denotes the
larger component of which the compartment is a member. Specific compart-
ments within components are denoted by the hyphenated capital letter
following the component number. In the case of a compartment that con-
sists of two or more sections, the compartment number will further
contain a section number in Arabic numerals, as is the case with Compart-
ment I-C of Figure 1 that possesses Sections I-C1 and I-C2.

Interactions between components and compartments

49. The arrows that run between the various components and compart-
ments in Figure 1 represent interactions occurring between and among the
various constituents of the model. The direction of an interaction is
indicated by an arrow. The number closest to an arrow designates the
interaction number. Double-headed arrows indicate two-way interactions.

50. When reference is made to an interaction, the interaction
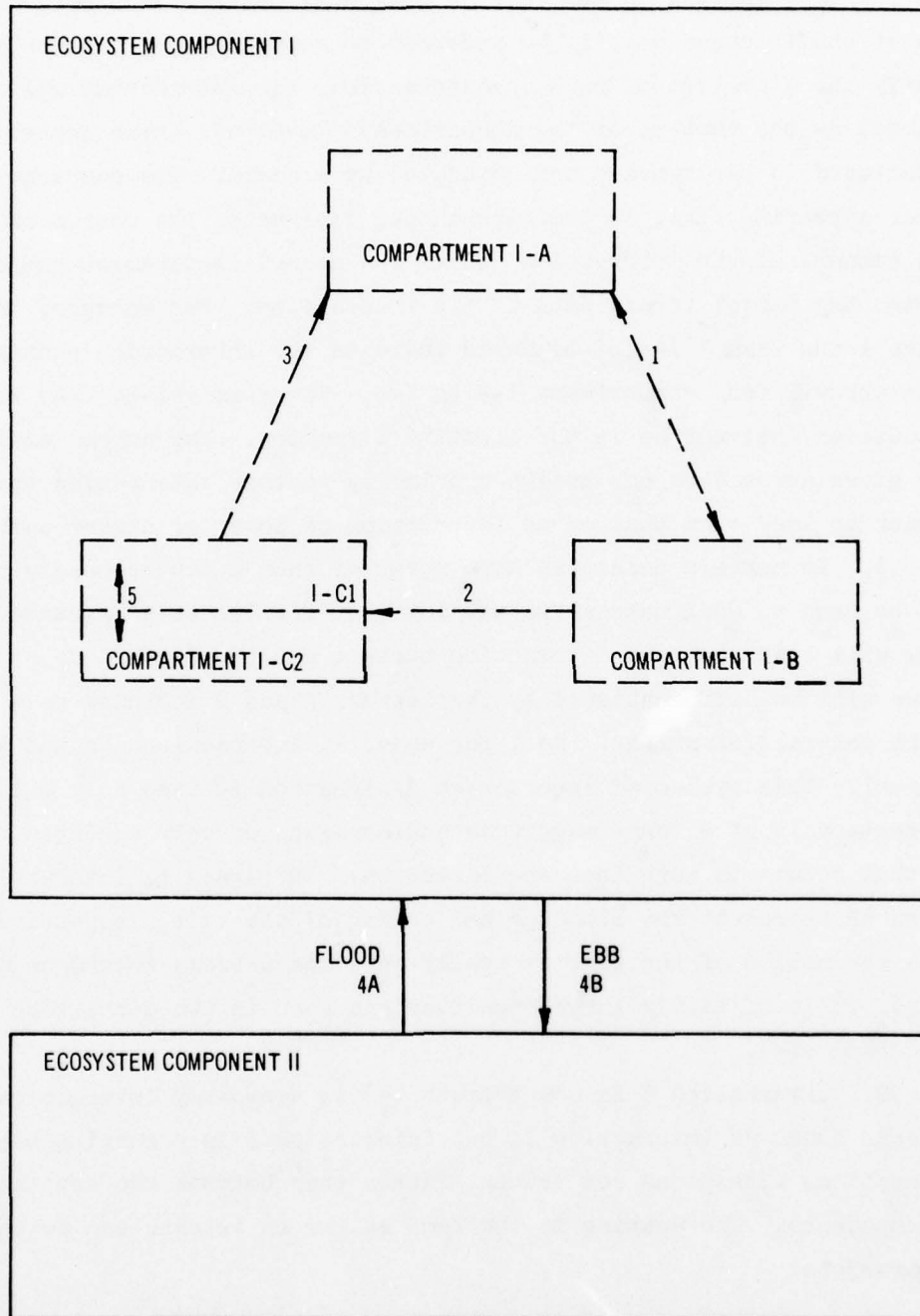
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Figure 1. Format used for construction of diagrammatic compartmental model. Labels in bold face type are ecosystem components or events occurring between components. Compartments within a component are outlined with dashed lines. Solid arrows represent interactions between components. Dashed lines are interactions within compartments or between compartments. Details are in text

number will be used. In the case of a two-way interaction, each direction of the interaction will be referred to separately. In order to specify the direction of such an interaction, the interaction will be followed by the numbers of the compartments involved; these numbers will be enclosed in parentheses and separated by a comma. The compartment number appearing first in the parentheses designates the source or origin (donor) of the interaction, while the second compartment number denotes the target (recipient) of the interaction. For example, in Figure 1 the term 1(I-A, I-B) would indicate the interaction running along arrow 1 from compartment I-A to I-B. The term 1(I-B, I-A) would indicate an interaction in the opposite direction. The number assigned to a given arrow does not assign a priority to that interaction that is greater or less than that of an interaction of lower or higher number.

51. In certain cases two arrows rather than a double-headed arrow will be used to designate a two-way interaction. In this instance, each arrow will bear the same interaction number, but the directions of the arrows will be differentiated by the letters A and B included as a part of the interaction number. See, for example, interactions 4A and 4B in Figure 1. This system of interaction designation is used only when an interaction is of a large magnitude and consists of only a single process that occurs in more than one direction. In Figure 1, interactions 4A and 4B represent the flooding and ebbing of the tide, respectively. While the motion of the tide is really only one process (movement of water), it is of fairly large magnitude and runs in two directions (flood and ebb).

52. Interaction 5 in Compartment I-C is a two-way interaction in the same sense as interaction 1, but interaction 5 is occurring between two sections within one compartment rather than between two compartments or components. The meaning is the same as for an interaction between compartments.

Components and Compartments of the Model

53. The details of the general compartmental model are presented in Figures 2 and 3. Figure 2 depicts the salt marsh ecosystem component

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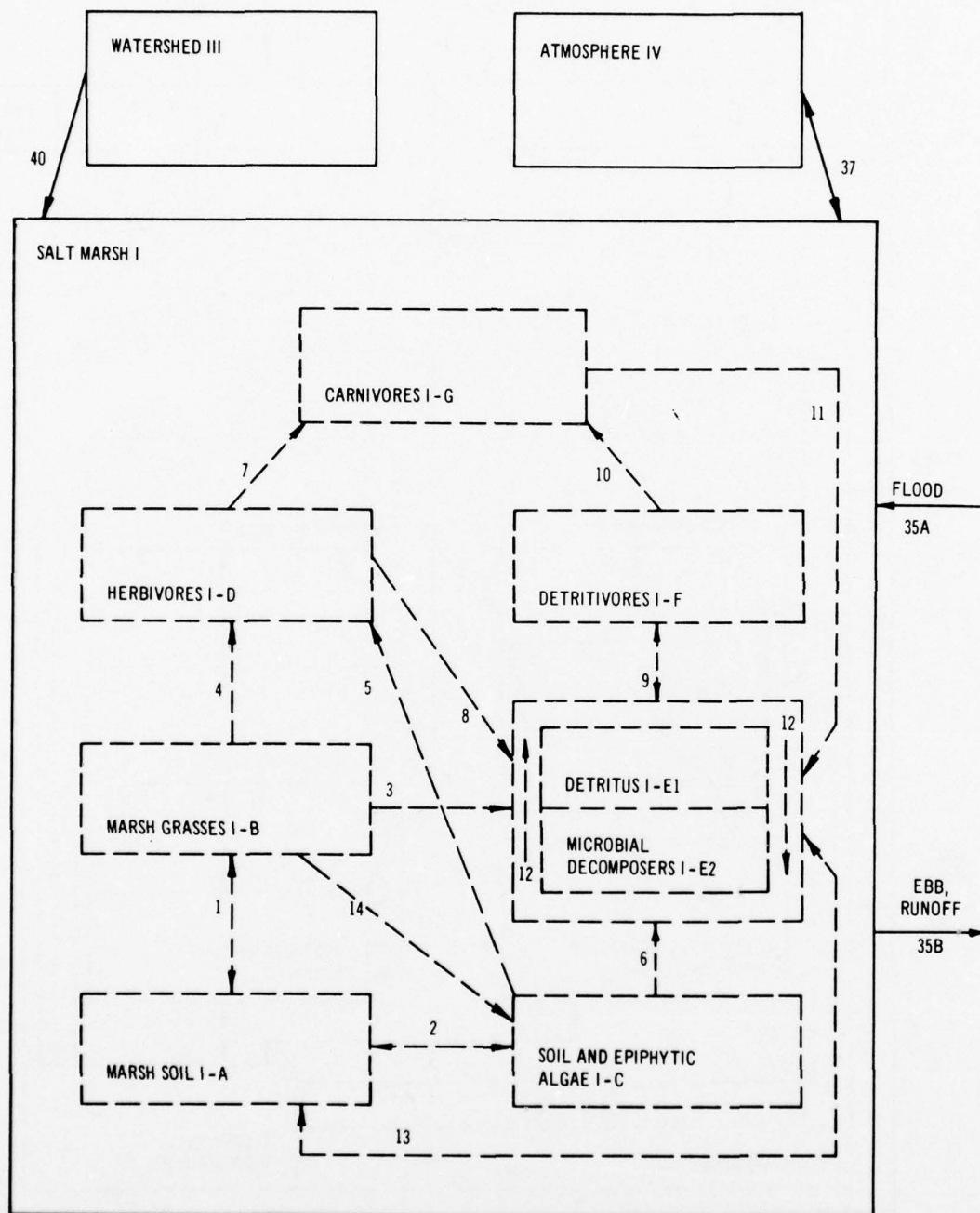
Figure 2. Salt marsh ecosystem component. For details of compartment
contents, see text. Table 1 gives a description of interactions
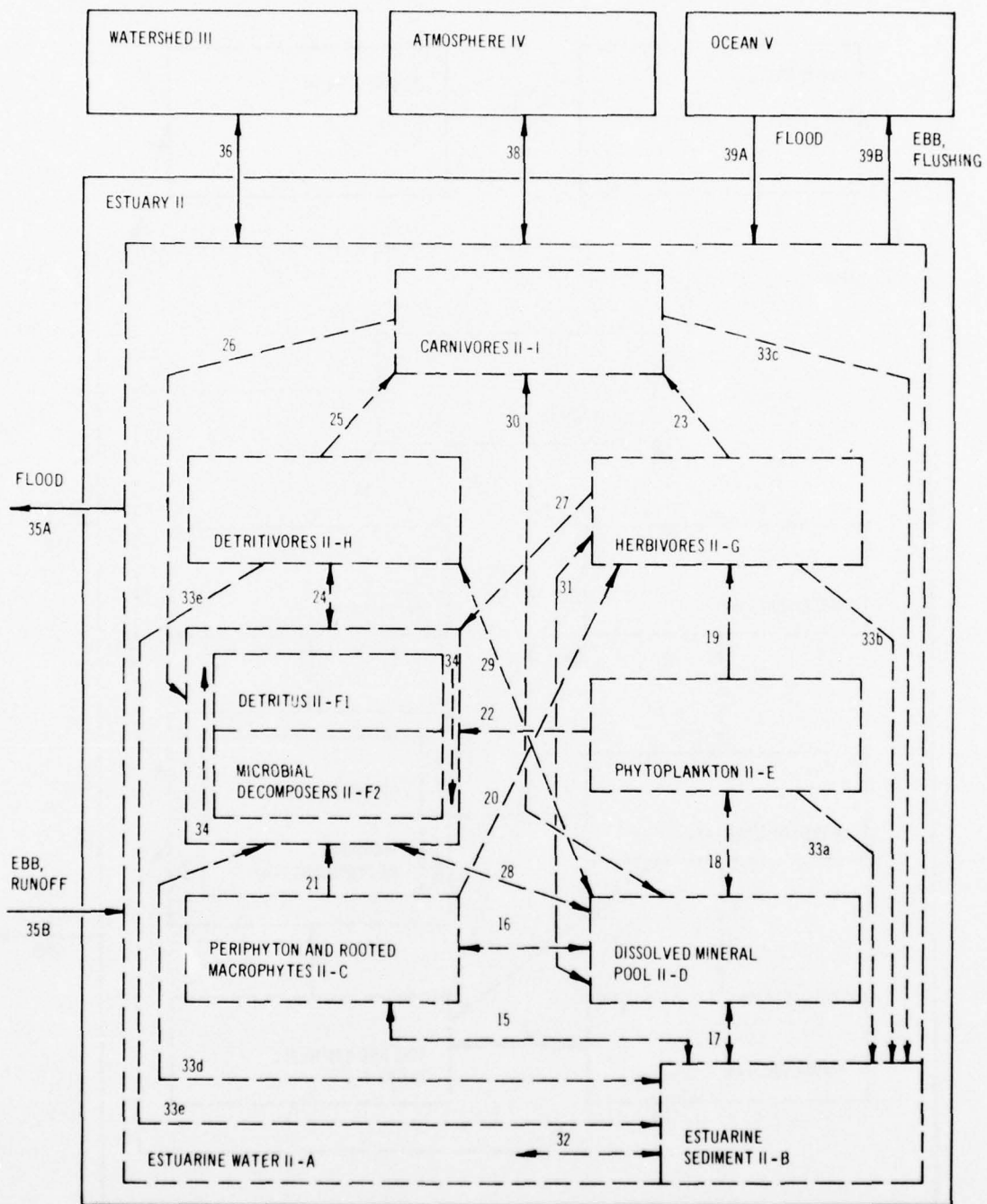
Figure 3. Estuary ecosystem component. For details of compartment contents, see text. Table 1 gives a description of interactions

along with the major links to other components that are vital to the functioning of the salt marsh. Figure 3 describes the estuary ecosystem component and gives the major links of this component with other components pertinent to estuarine ecology. The watershed (Component III), the atmosphere (Component IV), and the ocean (Component V) ecosystem components were not the major concern in this study and, thus, were not refined enough to require detailed compartmentalization.

Salt marsh ecosystem component

54. The salt marsh ecosystem component (Component I) houses a total of seven different compartments including: marsh soil (I-A), marsh grasses (I-B), soil and epiphytic algae (I-C), herbivores (I-D), detritus-microbial decomposers (I-E1, I-E2), detrivores (I-F), and carnivores (I-G).

55. When tidal waters flood the marsh (arrow 35A), the salt marsh and estuarine components are effectively joined to form a continuous ecosystem. At this time, the salt marsh component will acquire three additional compartments from the estuary component including: estuarine water (II-A), dissolved mineral pool (II-D), and phytoplankton (II-E).*
In addition, the compartments of the marsh component that have corresponding compartments in the estuary component may be modified at high tide to contain a few estuarine representatives of the same category.
For example, the brown shrimp Penaeus aztecus is normally an estuarine inhabitant that feeds largely upon detritus. As a result, this organism should be classified as a member of estuary ecosystem Component II, detritivore Compartment II-H. However, when the high tide moves up onto the marsh, Penaeus may move with it in order to browse upon the detritus lying on the marsh surface. At this point Penaeus might technically be considered a member of salt marsh ecosystem Component I, Detritivore Compartment I-F. Also, some fish (Fundulus heterclitus) enter the marsh to feed (Vince et al., 1976). Many other constituents of the estuary

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* As will be noted later in this paper, the intimacy of compartments at high tide is such as to permit an exchange of substances between the marsh and the estuary. Some substances, for example, nitrogen, show a net export from the marshes.

will participate in the same phenomenon. For simplicity, however, any organism or material that tends to remain chiefly within a single component will be considered as a permanent member of that component regardless of temporary translocations.

56. Compartment I-A. Compartment I-A of the salt marsh is the marsh soil. While the exact composition of marsh soil varies extensively both within the same marsh system and among different salt marshes, a marsh soil may be generally considered to consist of sand, silt, clay, and varying amounts of organic matter in the form of peat and humic acids (Kurz and Wagner, 1957; Teal and Teal, 1969; Chabreck, 1972; Ranwell, 1972). While the muds and sands can come from terrestrial, riverine, estuarine, or marine sources, the soil organic substances are mainly formed within the ecosystem. The amount and nature of organic materials in the soil is dependent upon: the geographical situation of the marsh site; the types and productivity of plant species growing at the site; in situ decompositional capacity of the site; the geological age and history of the site; and the meteorologic, erosive, and tidal characteristics of the site (Alexander, 1961; Buckman and Brady, 1969; Chabreck, 1972; Ranwell, 1972).

57. Compartment I-B. Marsh grasses form Compartment I-B of the salt marsh ecosystem component. Marsh grasses, like their terrestrial counterparts, may be considered as plants of the family Graminae, which includes plants having jointed stems, sheathed leaves, flowers borne on spikelets, and fruits consisting of seedlike grains (Hitchcock, 1971). The salt and brackish water grasses differ from their freshwater and upland counterparts in their ability to tolerate saline conditions. It is probably the tolerance of saline conditions rather than a strict requirement for salt water that is responsible for their coastal distribution. Most salt-adapted plants are unable to successfully compete with other plants in nonsaline environments (Uphof, 1941; Reimold and Queen, 1974). There are many species of marsh plants that are important in the marsh-estuarine ecosystem. However, for the sake of brevity, the present general discussion will be limited to the grass Spartina alterniflora, which is important in Gulf Coast marshes and is the dominant

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species along Atlantic Coast marshes (Adams, 1963; Teal and Teal, 1969; Stowe et al., 1971; Chabreck, 1972; Day et al., 1973; de la Cruz, 1973). Available data for other marsh grasses are given in Appendix A.

58. <u>Compartment I-C.</u> Compartment I-C includes the soil and epiphytic algae. The soil algae (the edaphic algae of Gallagher, 1974; Van Raalte et al., 1974) consist of those species that live within or on the marsh soil surface. Algae living within the soil are most commonly diatoms, while the surface forms include green and blue-green algae in addition to diatoms and others (Hustedt, 1955; Pomeroy, 1959; Stowe et al., 1971; Brkich, 1972). Many of these algae are also representative of the epiphytic algal community, i.e., those algae that attach themselves to and grow upon the marsh grasses. Many of these forms are intertidal or estuarine organisms that because of the frequency of tidal inundation, are able to extend their domain into the marsh. Some algae, typically diatoms, migrate into and out of the base marsh soil, moving out at the onset of flood tide and burying themselves in the mud at low tide in order to prevent direct exposure to the overly strong summer sun that may damage their photosynthetic processes. This situation is eliminated during the less intensive sunlight of winter when the algae usually remain on top of the mud (Teal and Teal, 1969). In New England marshes, however, diatoms move into the sand at high tide and during the night, coming to the surface only at low tide and in the daylight during cloudy weather; these organisms are able to do this because of the relatively lower intensity of the New England summer sunlight (Teal and Teal, 1969). During the marsh growing season, algal growth in the grassy areas of the marsh containing a canopy of marsh plants is limited by light. During the winter, however, when the aerial portions of the marsh plants have died back, light no longer limits algal production.

59. Evidence has been found that suggests that some soil algae float as a film upon the surface of the flood tide (Gallagher, 1956); they conduct their activities on this surface and subsequently return to the soil surface as the tide moves out.

60. <u>Compartment I-D.</u> Compartment I-D contains the salt marsh

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herbivores, those organisms that obtain most of their food directly
from the marsh primary producers (algae, marsh plants). Many of the
other organisms in Compartment I-D are not truly herbivorous. Indeed,
many of the marsh-estuarine animals are not strict herbivores, detri-
tivores, or carnivores, but instead are opportunists, i.e., omnivores
that are able to consume and use any of the appropriate-sized organisms
or organic particulates that they happen across. In addition, season
can have much to do with the types of food that are available. For the
purposes of this report, the various categories of herbivore, detriti-
vore, and carnivore serve as functional definitions to describe the food
that comprises the bulk of the intake of the organisms. In many cases,
the organism classified as an herbivore will secondarily feed on detri-
tus, which is mainly a plant product. The dominant marsh herbivores are
insects that graze on the grasses and the snails that feed on the algal
mats (Smalley, 1958). Raccoons, muskrats (nutria in the gulf Coast
marshes), ducks, and geese feed upon roots and rhizomes of marsh grasses
while several bird species consume the seeds of the various grass
species (Teal and Teal, 1969; Chabreck, 1972; Day et al., 1973).

61. _Compartment I-E._ Compartment I-E represents the detritus-
microbial decomposer unit of the salt marsh ecosystem component. Al-
though this compartment is considered as a single unit, it possesses two
functional subdivisions, the organic particles and the decomposer micro-
organisms attached to these particles. Detritus consists of all types
of materials of biological origin in various stages of biological decom-
position. These materials serve as energy sources for the consuming
organisms (detritivores). Detritus encompasses all dead organisms (in-
cluding dead decomposer microorganisms) together with all subsequent
particulate decomposition products that still represent potential energy
sources (Darnell, 1967a; Mann, 1972). The decomposer microflora is it-
self a potential energy source, and these organisms often form the bulk
of the critical or usable portion of organic detritus (Newell, 1964;
Fenchel, 1970).

62. Detritus is often divided into subcategories based upon size.
One of the more common fractionation schemes involves: (a) "particulate

organic detritus," which is considered as that material retained by filters having a pore diameter in the 0.2- to 2.0-µ size range, and (b) "subparticulate organic detritus," which is composed of colloidal and dissolved organic material that is able to pass through these filters (Holm-Hansen, 1972; Sharp, 1973).

63. Many of the organisms that function as the "microbial decomposers" (Compartment I-E2) are intimately associated with the decomposing substrates. The decomposer microflora help to increase the nitrogen content of detritus (often in the form of microbial cellular protein) to the point where detritus can serve as a nitrogen source of substantial nutrient value (Mann, 1972; de la Cruz, 1973). Marsh grasses and algae often have high carbon-to-nitrogen ratios with the former material often being so nitrogen-poor as to be unsuitable as a food source (de la Cruz, 1973). Decomposing microorganisms acting upon dead marsh vegetative materials can decrease the substrate carbon-to-nitrogen ratio by two mechanisms including: (a) metabolism of organic matter with subsequent loss of carbon as CO_2, while retaining substrate nitrogen either in the substrate (nonutilization) or incorporating the nitrogen into microbial cellular materials (immobilization); and (b) concentration of free nitrogen compounds (ammonium, nitrate, amino acids, etc.) from the ambient aquatic environment followed by incorporation of this nitrogen into cellular materials (Alexander, 1961; Thimann, 1963). In either case, little or no nitrogen from the substrate is excreted as waste products by the microflora until the carbon-to-nitrogen ratio has declined to a favorable level (Alexander, 1961).

64. Compartment I-F. The detritivore compartment contains those organisms that obtain their nutrition primarily from detritus particles and the decomposition products and the attached decomposer microflora sorbed or attached to the detritus. As a result of their food sources, the detritivores are primarily filter feeders and scavengers. Because of their ability to utilize substrates, which would otherwise be lost to processes of decomposition, and to "package" the nutrients so obtained into a form usable by other organisms (carnivores), the detritivores form the base of a secondary food chain (Lindeman, 1942).

Moreover, detritus feeders also comminute detritus, thus increasing the surface to volume ratio, thereby increasing decomposition rates. In the marsh-estuarine ecosystem, the detritus-based food chain is the major mechanism by which marsh primary production is exploited (Mann, 1972). While there are only two or three marsh-estuarine species that may be considered to be true detritivores in the sense that they obtain all of their nutrition from detritus (Odum, 1970), many species are so classified because they derive a minimum of 20 percent of their sustenance from detritus (Odum, 1970; de la Cruz, 1973).

65. Compartment I-G. Compartment I-G contains those carnivores that are secondary consumers. Their foods consist of live prey drawn from the herbivore (I-D) and detritivore (I-F) compartments and, often, other carnivores (tertiary consumers) (I-G). While some marsh animals are carnivorous, the majority of the carnivores having an impact upon marsh inhabitants are estuarine species that hunt in the marsh during flood tides or terrestrial species that move onto the marsh at low tide.

Estuary ecosystem component

66. Figure 3 depicts the water of the estuary as compartment II-A; this compartment envelopes each of the other compartments in the estuarine ecosystem component. In addition, the water of the estuary is always in intimate contact with the sediment (Compartment II-B) surface directly and, more remotely, with the lower sediment layers by way of interstitial waters. The remaining seven compartments of the estuary ecosystem component are either dissolved or suspended in, project into, or swim actively in the estuarine waters.

67. Compartment II-B. Compartment II-B represents the sediments of all parts of the estuarine basin up to the elevation at which these become exposed at extreme low tide. Estuarine sediments, like the marsh soil, have unique sets of organic and inorganic properties that are determined by local geographic, geologic, and physical characteristics. The three major components of the sediments (or sections of the compartment) include: (a) the organic fraction that consists of peats and/or deposits of detritus, biologically produced pseudofeces and feces, and/or humates; (b) the inorganic fraction composed of sands, silts, and

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clays; and (c) the interstitial waters, the water situated between the various particles of sediment. The sediments differ from the marsh soils in their lack of air spaces and their lower level of organic matter resulting from being situated downstream from rather than underlying an active zone of growing, dying, and decomposing grass plants. At this point, it should be emphasized that the tidal creeks are also considered a part of the estuary. However, because of their proximity to the detritus-producing salt marshes, the organic levels in tidal creek sediments will more closely approximate the amounts in the marsh soils than do those of the sediments in the main body of the estuary. Nevertheless, an estuarine sediment that formed from materials contained in a submerging marsh or supported a dense bed of sea grass (Zostera spp. or Thalassia) or macro-algae can have a high content of organic materials. In no case, however, does the estuarine sediment organic content rival that of the marshes where levels of over 50 percent can be achieved (Chabreck, 1972).

68. Compartment II-C. Compartment II-C contains the periphyton and rooted macrophytes. Periphyton, or attached algae, contain both microscopic and macroscopic forms. The microscopic forms occur both individually and in colonies and are attached to the bottom sediment surfaces or to materials situated on the bottom, including rocks (epilithic algae) and the rooted macrophytes (epiphytic algae). Submerged rooted macrophytes, by contrast, are those plants that are macroscopic in size and have special structures (basal cells) adapted for attachment of the organism either to the bottom sediments or to rocks situated on the bottom of the estuary. Examples of such plants include Zostera, Fucus, and Ulva (where solid peat permits attachment), and Ruppia (where freshwater springs emerge).

69. Compartment II-D. Compartment II-D, the dissolved mineral pool, is an extension of the water compartment II-A, in which the materials are dissolved. This compartment is separated because of the importance of its constituents to the other members of the marsh and estuarine ecosystem components. The dissolved mineral pool contains all materials, organic or inorganic, dissolved in the estuarine water column.

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In addition, all materials that exist in the water in colloidal form are included in this compartment. The primary materials so involved include the organic humates and the inorganic clays. The dissolved mineral pool contains substances of riverine, marine, and marsh origin as well as those native to the estuary.

70. Compartment II-E. The phytoplankton is contained in compartment II-E. In this compartment are placed all species of algae and photosynthetic bacteria that (a) float freely in the estuarine water column; (b) are subject to movement by estuarine currents; and (c) conduct their photosynthetic activities in the water column. The true member of the estuarine phytoplankton must (a) be a member of an autochthonous population that normally grows and multiplies within the estuary, or (b) a member of an allochthonous marine, freshwater, or marsh population that not only survives the rigors of movement into the estuary but also multiplies to an extent sufficient to maintain its population size while in the estuary (Perkins, 1974). Ill-adapted organisms are flushed from the estuary into the ocean before any significant population size can be achieved.

71. While the particular algae that are dominant in a given estuary or portion of an estuary will vary with the particular physical and chemical conditions existent in that estuary, diatoms and dinoflagellates tend to dominate the phytoplankton of most estuaries during much of the year (Riley, 1967; Perkins, 1974). Generally, major blooms occur in spring (actually late winter) and autumn. Phytoplankton are scarcer during the remainder of the year (Riley, 1967).

72. Compartment II-F. Compartment II-F, the detritus-microbial decomposer compartment, is very much like its marsh ecosystem component counterpart except that the estuarine detritus has a greater variety of sources, including marsh grasses, phytoplankton, rooted macrophytes, and minor contributions from dead animals. While there are many viewpoints concerning the inclusion of inorganic materials in the detritus category (Duursma, 1960; Krey, 1967), inorganic particulates serve as a site for attachment and growth of many aquatic microorganisms (Alexander, 1971). In addition, dissolved organic materials are sorbed by many inorganic

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particulates, thus changing the character of the inorganic particles to a more organic nature (Duursma, 1960).

73. <u>Compartments II-G, II-H, and II-I.</u> The herbivore, detritivore, and carnivore compartments (Compartments II-G, II-H, and II-I, respectively) have a function identical to that of their marsh ecosystem counterparts, except that (a) the detritivores and herbivores must obtain their materials from the water column or from deposits brought in by water and settled on the bottom, and (b) the carnivores living in the water column must be highly opportunistic, searching out and hunting down food both in the water column and on the sediment surface. Moreover, estuarine carnivores, especially fish, have a closely partitioned food web. This often involves more than the use of other animals as food sources. For example, <u>Menidia</u> is a diurnal plankton feeder, while <u>Fundulus heteroclitus</u> feeds predominantly on the salt marsh benthos.

Interactions between
components and compartments

74. Table 1 presents a detailed listing of the interactions occurring between the various components and compartments in Figures 2 and 3. As is summarized in Table 1, the marsh soil (compartment I-A) provides the marsh grasses (compartment I-B) and the soil algae (compartment I-C) with nutrients, physical support, a site for attachments, or combinations thereof (arrows 1 and 2). In addition, the marsh soil serves as a staging area for detritus production by (a) providing an area for detritus processing upon which detritus can be incubated in wet, warm, and predominantly aerobic conditions; (b) providing a microbial inoculum from old detritus and from the soil itself for initiating the breakdown of new materials into detritus; and (c) providing a surface upon which detritivores involved in the shredding and tearing functions of detritus processing (amphipods, crabs, shrimp) can move (arrow 13). When the detritus has been fragmented into small, easily moved particles, it is subsequently suspended and removed by the ebbing tides (arrow 35B) and storm runoff into the estuary (Teal, 1962; Day et al., 1973). Alternatively, plant materials may be decomposed by microorganisms to more resistant compounds (Alexander, 1961, 1965). Such materials may also

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Description of Interactions Occurring Between Compartments

and Components in Figures 2 and 3

Interaction No.	Direction* From	To	Description of Interaction	References
1	I-A	I-B	Mineral uptake from marsh soil and soil interstitial water by marsh grasses	Kurz and Wagner, 1957 Adams, 1963 Broome et al., 1973
	I-B	I-A	Addition of organic particulates to soil upon death of plant roots and rhizomes	Kurz and Wagner, 1957 Teal and Teal, 1969 Chabreck, 1972
			Aeration of soil by conduction of O_2 to roots and diffusion from roots into soil	Teal and Kanwisher, 1961
2	I-A	I-C	Marsh soil forms surface for attachment of algae and matrix into which algae move	Day et al., 1973 Teal and Teal, 1969 Van Raalte et al., 1976a,b
	I-C	I-A	Addition of organic particulates to soil upon death of algal cells	Alexander, 1961
			Excretion of photosynthate by live algae	Hellebust, 1967
			Lysis and release of cellular materials from dead cells	Alexander, 1961
3	I-B	I-E	Death of marsh grasses contributes substrate to microbial decomposers for detritus production	Burkholder and Bornside, 1957 Odum and de la Cruz, 1963 Teal and Teal, 1969 de la Cruz, 1973
4	I-B	I-D	Consumption of marsh grass production by herbivores (including leaves, shoots, seeds, roots, and rhizomes)	Smalley, 1959, 1960 Teal and Teal, 1969 Day et al., 1973
5	I-C	I-D	Consumption of soil and epiphytic algae by herbivores	Smalley, 1959, 1960
6	I-C	I-E	Death of soil and epiphytic algae contributes substrates to microbial decomposers for detritus production	Darnell, 1967b Odum and de la Cruz, 1967
7	I-D	I-G	Predation of marsh herbivores by carnivores	Teal, 1962
8	I-D	I-E	Contribution of herbivore fecal materials to detritus pool	Kuenzler, 1961 Darnell, 1976
			Contribution of animal tissues to detritus pool upon death of herbivores	Darnell, 1976
9	I-E	I-F	Consumption of organic detritus by detritivore population	ZoBell and Feltham, 1938, 1942 Darnell, 1961 Darnell, 1967a&b Mann, 1972 de la Cruz, 1973
	I-F	I-E	Contribution of detritivore fecal material to detritus pool	Kuenzler, 1961 Darnell, 1967b
			Contribution of animal tissues to detritus pool upon death of detritivores	Darnell, 1967b
10	I-F	I-G	Predation of marsh detritivore population by carnivores	Teal and Teal, 1969 Teal and Teal, 1969
11	I-G	I-E	Contribution of carnivore fecal material to detritus pool	Darnell, 1976
			Contribution of animal tissues to detritus pool upon death of detritivores	Odum and de la Cruz, 1967
12	I-E1	I-E2	Decomposition of detritus substrate supplies, minerals, and energy to decomposer microflora	Burkholder and Bornside, 1957 Darnell, 1967a,b Odum and de la Cruz, 1967 Mann, 1972
	I-E2	I-E1	Contribution of metabolites and microbially produced decomposition products to detritus	Darnell, 1967a,b Mann, 1972 de la Cruz, 1973
			Contribution of dead microbial cell tissue to detritus pool	Darnell, 1967 a&b Mann, 1972 de la Cruz, 1973
13	I-A	I-E	Detritus pool existing on marsh surface serves as as inoculum for new detrital substrates**	Burkholder and Bornside, 1957
	I-E	I-A	Detritus not flushed from marsh surface by tides becomes incorporated with soil as a part of soil organic matter	Teal, 1962
14	I-B	I-C	Marsh grasses serve as a substrate for attachment of epiphytic algae	Day et al., 1973
			Marsh grasses shade out soil and epiphytic algae and decrease their growth within marsh during the normal grass growing season	Day et al., 1973

(Continued)

* See text for explanation of details.
** Inferences made from general statements.

Table 1 (Continued)

Interaction No.	Direction From	To	Description of Interaction	References
15	II-B	II-C	Estuarine sediment provides an attachment substrate for periphytic algae and rooted macrophytes	Kelley et al., 1971
			Mineral uptake from estuarine sediment and interstitial water by rooted macrophytes	McRoy and Barsdate, 1970 Zieman, 1975
	II-C	II-B	Addition of organic particulates to sediments upon death of rooted macrophyte root systems and leaves	Zieman, 1975
			Excretion of dissolved organic materials and sloughing of root materials by macrophyte roots add to sediment organic matter pool	This has not been studied for estuarine macrophytes
			Macrophyte roots stabilize sediments	Kelley et al., 1971
16	II-C	II-D	Excretion of dissolved inorganic and organic materials by periphyton and rooted macrophytes	Khailov and Burlakova, 1969 Sieburth and Jensen, 1969 Chapman and Rae, 1969 Riley, 1970
	II-D	II-C	Sorption by leaves of rooted macrophytes and by periphyton of inorganic materials from dissolved mineral pool	McRoy and Barsdate, 1970
17	II-B	II-D	Diffusion of dissolved materials out of sediments (via interstitial water) into the dissolved mineral pool in estuary water	Ho, 1971 Ho and Lane, 1973 Ho et al., 1970
	II-D	II-B	Diffusion of dissolved materials from the dissolved mineral pool into sediments (via interstitial water)	Ho and Lane, 1973 Khalid et al., 1975
			Sorption of materials to sediment surfaces	Ho et al., 1970 Khalid et al., 1975
18	II-D	II-E	Mineral uptake from dissolved mineral pool by phytoplankton	Lund, 1965
	II-E	II-D	Release of minerals and dissolved organic matter from phytoplankton by excretion and/or autolysis	Hellebust, 1967 Lund, 1965
19	II-E	II-G	Consumption of estuarine phytoplankton by herbivores	Riley, 1967
20	II-C	II-G	Consumption of estuarine periphyton and rooted macrophytes by herbivores	Thayer et al., 1975
21	II-C	II-F	Contribution of periphyton cells and macrophyte leaf tissues to detritus pool upon death of plants	Mann, 1972
22	II-E	II-F	Contribution of phytoplankton cells to detritus pool upon death of algae	Mann, 1972
23	II-G	II-I	Predation of estuarine herbivore population by carnivores	Darnell, 1961 Riley, 1967 Caperon, 1975
24	II-F	II-H	Consumption of organic detritus by detritivore population	ZoBell and Feltham, 1942 Darnell, 1961 Darnell, 1967a,b Mann, 1972 de la Cruz, 1973
	II-H	II-F	Contribution of detritivore fecal material to detritus pool	Kuenzler, 1961 Darnell, 1967a,b
			Contribution of animal tissues to detritus pool upon death of detritivores	Darnell, 1967a,b
25	II-H	II-I	Predation of estuarine detritivore population by carnivores	Darnell, 1961
26	II-I	II-F	Contribution of carnivore fecal material to detritus pool	Darnell, 1967b
			Contribution of animal tissues to detritus pool upon death of carnivores	Darnell, 1967b
27	II-G	II-F	Contribution of herbivore fecal material to detritus pool	Darnell, 1967b
			Contribution of animal tissues to detritus pool upon death of herbivores	Darnell, 1967b
28	II-D	II-F	Uptake of minerals by microbial decomposers from dissolved mineral pool	Krey, 1967 Newell, 1964
			Sorption of materials from dissolved mineral pool by detritus	Darnell, 1967b
	II-F	II-D	Release of minerals and dissolved organic matter to dissolved mineral pool by:	
			(a) Extracellular digestion of detritus by microbial decomposers	Darnell, 1967b Gunnison and Alexander, 1975a&b

(Continued)

Table 1 (Concluded)

Interaction No.	Direction From	To	Description of Interaction	References
28 (Continued)			(b) Excretion of metabolites and excessive ions by microbial decomposers	Thimann, 1963
			(c) Autolysis of microbial decomposers and detrital tissues	Golterman, 1964
29	II-D	II-H	Uptake of minerals by detritivores--largely due to osmotic differences associated with life in salt water	Gordon, 1972
	II-H	II-D	Release of minerals and dissolved organic matter (primarily urea) by excretion of detritivores	Various physiology texts, i.e., Prosser and Brown, 1961
30	II-D	II-I	Uptake of minerals by carnivores--largely due to osmotic differences associated with life in salt water	Gordon, 1972
	II-I	II-D	Release of minerals and dissolved organic matter (primarily urea) by excretion of carnivores	Various physiology texts, i.e., Prosser and Brown, 1961
31	II-D	II-G	Uptake of minerals by herbivores--largely due to osmotic differences associated with life in salt water	Gordon, 1972
	II-G	II-D	Release of minerals and dissolved organic matter (primarily urea) by excretion of herbivores	Various physiology texts, i.e., Prosser and Brown, 1961
32	II	II-B	Sedimentation of inorganic materials from the water column to surface of bottom sediments	Darnell, 1967b Perkins, 1974
33	Several Compartments	II-B	Settling of dead materials onto surface of bottom sediments from each of the following compartments: 33a Phytoplankton (II-E) 33b Herbivores (II-G) 33c Carnivores (II-I) 33d Detritus-Microbial Decomposers (II-F) 33e Detritivores (II-H)	Day, 1952
34	II-F1	II-F2	Decomposition of detritus substrate supplies, minerals, and energy to the decomposer microflora	Burkholder and Bornside, 1957 Darnell, 1967a,b Odum and de la Cruz, 1967 Mann, 1972
	II-F2	II-F1	Contribution of metabolites and microbially released decomposition products to detritus	Darnell, 1967a,b Mann, 1972
			Contribution of dead microbial cell tissue to detritus pool	de la Cruz, 1973
35A	II	I	Flood tide estuary waters and attendant organisms, dissolved minerals, and particulate matter move onto marsh	Teal and Teal, 1969
35B	I	II	Ebb tide waters and attendant organisms, dissolved minerals, and particulate matter move off of marsh	Teal and Teal, 1969
36	II-A	III	Watershed adds fresh water and particulate matter to estuary	Reid, 1961 Perkins, 1974
37	I	IV	Marsh contributes gaseous products of respiration, photosynthesis, and decomposition to atmosphere	Teal and Kanwisher, 1961
	VI	I	Atmosphere contributes gaseous requirements for respiration, photosynthesis, and N-fixation to the marsh	Teal and Kanwisher, 1961 Teal and Teal, 1969
	VI	I	Rain erodes marsh at low tide	Teal and Kanwisher, 1961 Teal and Teal, 1969
38	II-A	IV	Estuarine water contributes gaseous products of respiration, photosynthesis, and decomposition to atmosphere	Kanwisher, 1963 Teal and Kanwisher, 1961
	IV	II-A	Atmosphere contributes gaseous materials needed for respiration, decomposition, photosynthesis, and N-fixation to estuarine water	Kanwisher, 1963 Teal and Kanwisher, 1961
39A	V	II-A	Saltwater intrusion moves organisms, dissolved minerals, and particulate matter into estuary from ocean	Reid, 1961
39B	II-A	V	Normal currents flowing through estuary and ebb tide estuary waters and attendant organisms, dissolved minerals, and particulate matter move into ocean although estuary traps many nutrients	Reid, 1961 Perkins, 1974
40	III	I	Springs come up in marsh	Personal communication, April 1975, John Teal, Ecologist, Woods Hole Oceanographic Institution, Woods Hole, MA. Personal communication, April 1975, Ivan Valiela, Associate Professor, Woods Hole, MA.

enter estuaries in tidal and storm runoff or may be incorporated into the soil organic matter.

75. Both fresh and estuarine water may interact with marsh soils. Fresh water may form a true water table beneath the marsh, coming from terrestrial environments and debouching upon lower lying areas, such as tidal creeks (arrow 40). Alternatively, fresh waters may surface at various locations in the marsh forming actual springs that then run over the marsh surface to various marsh channels (Personal Communication, April 1975, John Teal, Ecologist, Woods Hole Oceanographic Institution, Woods Hole, Mass.; Personal Communication, April 1975, Ivan Valiela, Associate Professor, Woods Hole, Mass.). Finally, fresh water may enter from the atmosphere as rain or snow (arrow 36) and, under the proper conditions, move through the soil. Under any condition, the movement of fresh water through salt marsh soil will leach out deposited salts.

76. Arrows 35A and 35B. The ebbing and flooding of tides over the marsh surface exerts influences in addition to deposition and removal of materials. Tidal waters exchange dissolved materials with the interstitial waters of the marsh soil. The amount, rate, and form of the materials exchanged are largely determined by the composition of the soil. All other factors being the same, a sandy soil tends to have more of its void volume replaced by tidal waters than does a soil with a high organic and clay content. Thus, the plants growing in a sandy soil are more largely influenced by nutrients borne in tidal waters than are plants in a more organic-clay soil. Composition also determines the amount of air contained in marsh soil, especially at low tide.

77. Arrows 1, 2, 3, 4, and 14. Marsh grasses (compartment I-B) interact with four other salt marsh compartments (I-A, I-C, I-D, and I-E). In addition, marsh grass interacts with the tidal waters (compartment II-A of the estuarine ecosystem component) and with the atmosphere (ecosystem component IV). The marsh soil provides grass with a firm substrate in which to anchor its roots for support purposes and also supplies the grass with nutrients required for growth and maintenance [arrow 1 (I-A, I-B)]. The marsh grass, in turn, supplies the soil with inorganic and organic materials released during metabolism or

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solubilized or sloughed from its roots and rhizomes [arrow 1 (I-B, I-A)].
In addition, death provides the marsh soil with plant roots and rhizomes
that become a part of the soil organic matter as a consequence of var-
ious decompositional processes [also arrow 1 (I-B, I-A)]. Some marsh
grass production is lost to compartment I-D, the herbivores (arrow 4).
In terms of total marsh grass production, however, this is minimal and
accounts for approximately 10 percent of the total production (Smalley,
1958; 1959). The remaining grass dies and becomes a part of the detri-
tus pool in the marsh (arrow 3), or is rafted out of the marsh into the
estuary by receding tides (compartment II-A, arrow 35B) to become a part
of the estuarine detritus pool (compartment II-F). Epiphytic algae (com-
partment I-C) depend upon marsh grasses at the edges of creekbanks and
other fringes of the marsh to supply the substrates to which they can
attach (arrow 14). Both epiphytic and soil algae depend on an abundant
supply of sunlight for their growth; therefore, in the denser areas of
marsh grass growth, both of these algal groups may become shaded out
(arrow 14).

78. Marsh grass exchanges with the atmosphere, ecosystem component
IV, [arrow 37 (IV, I) and 37 (I, IV)] include uptake of gases needed for
photosynthesis (during daylight hours) and respiration (day and night).
In turn, marsh grasses release gases produced during photosynthesis and
respiration and water vapor from transpiration [arrow 37 (I, IV)] back
to the atmosphere.

79. Whether the soil algae (compartment I-C) attach to the soil
surface or burrow into the soil matrix, an interaction is still indi-
cated (arrow 2). Other algal species attach to both soil and marsh
grasses (arrow 14). Soil algae undergo gaseous exchanges with the
atmosphere [arrow 37 (I, IV) and 37 (IV, I)]. However, most algal nu-
trients are obtained from flood tide waters (35A) into which metabolic
wastes are eliminated and carried away by ebbing tides (35B).

80. Soil algae are an important source of energy and nutrient in-
put into the marsh herbivore and detritus compartments (compartments I-D
and I-E, respectively) by grazing (arrow 5) or by death (arrow 6). Sev-
eral of the marsh invertebrates obtain a major portion of their food,

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either from the soil and epiphytic algae or from a mixture of these algae and the detritus located on the marsh soil surface (Day et al., 1973).

81. The detritus-microbial decomposer compartment (compartment I-E, sections 1 and 2) is a key compartment, because it interacts with all other compartments on the marsh as well as with portions of several other ecosystem components. Although all of the compartments that house biotic components of the marsh can contribute to the pool of detritus (arrows 3, 6, 8, 9, 11, and 12), the largest source of detritus is marsh grass that, in turn, is the largest producer on the marsh. Detritus can be consumed by the marsh detritivore population [arrow 9 (I-E, I-F)] or completely degraded into resistant materials that subsequently can become a part of the marsh soil [arrow 13 (I-E, I-A)]. However, an estimated 50 percent of the production will be exported to the estuary (arrow 35B), where it becomes a part of the detritus compartment (II-F) or settles to the bottom of the estuary (arrow 33d) to become deposited in the estuarine sediment (compartment II-B) (Teal, 1962; Day et al., 1973). Alternatively, this detritus may be carried out of the estuary by oceanward ebbing tides (39B) or be redeposited elsewhere on the marsh by subsequent flood tides (35A). The marsh-based detritus can also interact with the atmosphere component at low tide (arrow 37) by taking up oxygen required for aerobic decompositional processes (37 IV, I) and releasing carbon dioxide (37 I, IV).

82. The marsh herbivore compartment (I-D) has few direct interactions with the other marsh compartments. Herbivores do exert an indirect action on nitrogen supply through consumption of protein in grasses. Herbivores obtain food by grazing on marsh grasses (I-B) or algae (I-C) (arrows 4 and 5). Losses from the compartment occur through predation by carnivores (arrow 7), death (arrow 8), or defecation (arrow 8). The detritivore compartment also has few direct interactions with other marsh compartments. While detritus is the food source for these organisms [arrow 9 (I-E, I-F)], many of the organisms that are not consumed by predators (arrow 10) will themselves contribute to the detritus pool [arrow 9 (I-F, I-E)] either through their own death or by waste product production.

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83. Marsh carnivores (compartment I-G) depend on both the herbivores and the detritivores as sources of prey (arrows 7 and 10, respectively). The carnivores make minor contributions to the detritus-microbial decomposer compartment either through death or defecation (arrow 11). There is also some intracompartmental predation (cannibalism, consumption of lower carnivores by higher carnivores).

84. Reference is again made to Table 1 for the interactions occurring in Figure 3, the Estuary Ecosystem Component. While many of the interactions that occur in the estuary are identical to their marsh-based counterparts, the difference brought about by the suspension of many of the estuarine compartments in the water column is sufficient to warrant a separate consideration of the estuary.

85. Compartment II-B, the Estuarine Sediment, contains all the particulate matter located in the bottom (bed, basin) of the estuary. All those suspended inorganic materials are considered as suspended sediments (that portion of compartment II-B retained in estuarine water by action of arrow 32 (II-B, II-A). All suspended organic materials are considered as detritus (II-F).

86. The estuarine sediment receives inputs from several estuary components. Unsuspended detritus settles to the bottom of the estuary to serve as a nutrient and energy source for communities of the estuarine sediment [arrows 15 (II-C, II-B), 33a, b, c, d, and e]. Additional input to the estuarine sediment includes settling of inorganic suspended sediments from the water column [arrow 32 (II-A, II-B)]. Suspended sediments may be recruited from upstream in the watershed (arrow 36), by tidal and storm scouring from marsh surfaces (arrow 35B), through wind transport [arrow 38 (IV, II-A)], and, to a lesser extent, from flood tide input of oceanic debris (arrow 39A). Alternatively, suspended sediments may also originate by resuspension of estuarine sediments [arrow 32 (II-B, II-A)]. A final source of sediment materials is the formation of crystalline particulates from dissolved minerals (compartment II-D) followed by sedimentation of these materials from the water column [arrow 17 (II-D, II-B)].

87. The estuarine sediment has intimate relationships with the

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periphyton and submerged rooted macrophyte compartment (II-C). The sediment provides a support medium for the macrophytes and an attachment surface for the periphyton [arrow 15 (II-B, II-C)]. Whether the interstitial water in the estuarine sediment also provides macrophytes with nutrients in situ has not been established, although in vitro studies do indicate that macrophytes take up nutrients via this route (McRoy and Barsdate, 1970). Finally, both submerged macrophytes and periphyton may contribute particulate matter to the organic matter of the estuarine sediment [arrow 15 (II-C, II-B)].

88. The periphyton and submerged rooted macrophytes compartment (II-C) has four interactions with estuarine compartments other than those already enumerated for the sediment. Periphyton and leaf sections of submerged rooted macrophytes are able to take up needed nutrients and dissolved gases from the dissolved mineral pool [arrow 16 (II-D, II-C)]. In turn, these organisms resupply the dissolved mineral pool with organic matter and gaseous products resulting from their metabolic and photosynthetic processes [arrow 16 (II-C, II-D)]. Constituents of compartment II-C also supply (a) a source of estuarine-sediment based vegetation for herbivores (arrow 20) and (b) one of two estuarine-based sources of vegetative detritus (arrow 21).

89. The dissolved mineral pool (compartment II-D) is one of the principal focal points in the chemical environment of the estuary. All estuarine biotic and abiotic agents have some degree of interaction with this compartment. While all biotic agents take up at least some minerals from the pool [arrows 16, (II-D, II-C); 18 (II-D, II-E); 28 (II-D, II-F); 29 (II-D, II-H); 30 (II-D, II-I); and 31 (II-D, II-G)] and excrete some minerals or organic compounds back into the pool [arrows 16 (II-C, II-D); 18 (II-E, II-D); 28 (II-F, II-D); 29 (II-H, II-D); 30 (II-I, II-D); and 31 (II-G, II-D)], the abiotic agents also all make some contribution, albeit a passive role rather than an active one. Dissolved materials may be recruited by transport of mineral-bearing waters into the estuary (arrows 35B, 36, and 39A), by solubilization of gases from the atmosphere [arrow 38 (IV, IIA)], or by solubilization of minerals from either solid materials in the sediment [arrow 17 (II-B, II-D)],

or from solid materials brought into the estuary from upstream (arrow 36), from the marsh (arrow 35B), the atmosphere [arrow 38 (IV, II-A)], or the ocean (arrow 39A). Dissolved minerals may also be lost from the pool either after the formation of solid precipitates or flocculates or sorption to existing solids. These materials may then be moved out of the estuary by transport (arrows 35a, 39B) or sedimentation [arrow 32 (II-A, II-B)]. Alternatively, dissolved gases may diffuse into the atmosphere [arrow 38 (II-A, IV)].

90. Phytoplankton (compartment II-E) forms the second compartment of estuarine-based primary producers. Productivity of this compartment is governed not only by the level of nutrients available to it from Compartment II-D via arrow 18 (II-D, II-E), but also by the density of particulate materials in the water column from compartments II-B (suspended sediments), II-F (detritus), and even other phytoplankton, each of which may exert a shading influence with a resultant decrease in phytoplankton productivity. These same factors will influence the growth of the periphyton and rooted macrophytes (compartment II-C). Phytoplankton may be recruited from organisms brought into the estuary from upstream (arrow 36), from the oceans (arrow 39A), or from the marsh (arrow 35B). However, the bulk of the phytoplankton is composed of autochthonous species that multiply in the estuary.

91. Phytoplankton losses may occur through herbivore grazing (arrow 19), by death and subsequent loss of material to detrital pools (arrow 22), or by settling of phytoplankton cells to the bottom of the estuary (arrow 33a). The phytoplankton may also lose some of its cellular constituents as a result of the solubilization of cell wall material, loss of internal photosynthate by leaching or lysis, or by actual excretion of dissolved substances [arrow 18 (II-E, II-D)] (Gunnison and Alexander, 1975a and b).

92. Compartment II-F, the detritus-microbial decomposer compartment, functions in the same manner as its marsh counterpart (denoted by arrow 34), except that it has several other sources in addition to marsh grasses and soil and epiphytic algae including: periphyton and rooted macrophytes [arrows 21 and 33d (II-B, II-F)], phytoplankton (arrow 22),

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herbivores (arrow 27), detritivores [arrow 24 (II-H, II-F)], and carnivores [arrow 26 (II-I, II-F)]. In addition, ebbing tides and storm runoff flush a large amount of marsh detritus into the estuary (arrow 35B). This can represent a considerable proportion of the total detrital material in compartment II-F (Teal, 1962; Day et al., 1973; de la Cruz, 1973).

93. Detritus also has close ties with the dissolved mineral pool (compartment II-D). The microbial decomposers may remove needed nutrients and heavy metals plus dissolved gases from the mineral pool [arrow 28 (II-D, II-F)]. Additionally, the detritus portion itself may sorb many materials from the pool [also arrow 28 (II-D, II-F)]. The detritus decomposition processes add many products back into the mineral pool including dissolved gases and other metabolic wastes produced by metabolic activities of the decomposers, products solubilized during the extracellular decomposition of the detritus, and soluble cellular materials released upon autolysis of the decomposers [arrow 28 (II-F, II-D)].

94. Detritus may be lost from the system by one of four possible mechanisms including: (a) complete decomposition to soluble materials [via arrow 34 to arrow 28 (II-F, II-D)], (b) sedimentation to the bottom of the estuary (arrow 33d), (c) consumption by detritivores [arrow 24 (II-F, II-H)], and (d) flushing from the estuary into the ocean (arrow 39B). It is possible for flood tides to place some detritus back onto the marsh (arrow 35A), however, the amount of organic matter accumulated as peat per year is approximately two orders of magnitude lower than the net production of marsh grasses (Personal Communication, April 1975, Ivan Valiela, Associate Professor, University of Boston Marine Program, Marine Biological Laboratory, Woods Hole, Mass.). Moreover, Teal reports that he and his colleagues have measured significant capture of waterborne detritus by marshes (Personal Communication, April 1975, John Teal, Ecologist, Woods Hole Oceanographic Institution, Woods Hole, Mass.). Finally, a marsh having deep pools that can trap organic detritus may result in detritus of estuarine or coastal origins (such as from eel grasses) being retained in amounts albeit in amounts less than the export of _Spartina_ detritus (Woodwell et al., 1973). Most of the detritus remains entrained in

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Compartment II-F, moving back and forth with the tides until it is either decomposed, consumed, or sedimented (Personal Communication, December 1975, John Hall, Microbiologist, University of Georgia Marine Institute, Sapelo Island, Georgia).

95. The estuarine herbivore compartment (II-G) includes those animals that feed on periphyton, rooted macrophytes (II-C via arrow 20), and phytoplankton (II-E via arrow 19). In turn, herbivores serve as prey for carnivores (II-I via arrow 23) and, upon death, as a source of detritus (II-F via arrow 27) or other organic matter in the estuarine sediment (arrow 36b). While some herbivores, particularly algae-consuming protozoa, do take up minerals from the mineral pool [arrow 31 (II-D, II-G)], the larger interaction between these compartments occurs in the reverse direction [arrow 31 (II-G, II-D) through excretion of soluble organic and inorganic wastes.

96. Estuarine detritivores (compartment II-H) obtain most of their nutrition from the detritus compartment [arrow 24 (II-F, II-H)] and may obtain supplemental nutrients from the dissolved mineral pool [arrow 29 (II-D, II-H)]. The detritivore population may lose many members to predation (arrow 25), to death and decomposition [arrow 24 (II-H, II-F)], and to death and sedimentation (arrow 33e). Many detritivores, however, mature and migrate out of the estuary, either upstream into fresh water [arrow 36 (II-A, III)] or out into the ocean (arrow 39B). While the predominant teleological reason for such migration is to permit the species involved to spawn, few of the adults of any migrating species return to the estuary. Thus, much of the production is lost from the salt marsh-estuarine ecosystem and only a small portion of this returns in the form of new progeny (Perkins, 1974).

97. Carnivores (compartment II-I) migrate from the estuary to the watershed [arrow 36 (II-A, III)] or out into the ocean (arrow 39B). A few carnivores are lost to compartmental self-predation (not described), through death to detritus (arrow 26), or through death and sedimentation to the estuarine sediment (arrow 33c). While some substances (principally oxygen for respiration) are taken from compartment II-D [arrow 30 (II-D, II-I)], more of the materials are obtained from food; thus, the larger interaction described by arrow 30 runs from II-I to II-D.

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Finally, the carnivores also contribute to the detritus pool through their waste products (feces) via arrow 26.

Summary of Function of Compartmental Model
of the Marsh-Estuarine Ecosystem

98. The general compartmental model of the marsh-estuarine ecosystem describes the predominant constituents and processes in existing marshes. Since newly developing marshes are somewhat unpredictable, no attempt has been made to characterize them here. The following discussion places the previously described compartmental model within the context of a functional ecosystem.

99. Marsh soil (I-A) and the dissolved mineral pool (II-D brought in with flooding tide waters 35A) interact with air (IV) to supply minerals to the marsh grasses (I-B) and the soil and epiphytic algae (I-C) - the primary producers of the salt marsh ecosystem component (I). Marsh grasses and marsh algae are a food source for herbivores (I-D) while alive (arrows 4 and 5). However, the bulk of the production of these compartments dies and becomes a part of the marsh detritus pool (I-E by way of arrows 3 and 6). Detritus (I-E1) is continuously being degraded and modified (arrow 12) by the microflora (I-E2) into forms that are either utilized by marsh detritivore species [I-F by way of arrow 9 (I-E, I-F)] or are further decomposed into marsh soil organic matter [I-A by arrow 13 (I-E, I-A)]. Detritus that has been decomposed to small enough particles can also be suspended and carried off by outgoing tides (35B) to form a part of the estuarine detritus pool (II-F), where it is consumed by detritivores, settles to the bottom of the estuary as organic deposits (arrow 33d), or is mineralized [II-D by way of arrows 34 and 28 (II-F, II-D)].

100. Both the marsh herbivore and detritivore species (compartments I-D and I-F) can provide food for marsh carnivores (I-G by way of arrows 7 and 10). After death, the herbivores, detritivores, and carnivores become a part of the detritus compartment [I-E via arrows 8, 9 (I-F, I-E), and 11, respectively]. These marsh organisms may also serve as prey for those estuarine carnivores (II-I) that move onto and off the marsh with

each respective flood (35A) and ebb (35B) tide.

101. The estuarine ecosystem component has both benthic (II-C) and free-floating (II-E) sources of primary production.* While the estuarine sediment (II-B) is a source of nutrients for those plants that are intimately associated with it [II-C via arrow 15 (II-B, II-C)], the dissolved mineral pool [II-D by way of 16 (II-D, II-C) and 18 (II-D, II-E)] is a major source of nutrients for other primary producers. As was true for the marsh, the estuarine plants may either be grazed by herbivores (II-G via arrows 20 and 19), or the plants may die and become part of the estuarine detritus pool (II-F by way of arrows 21 and 22). Detritus may be consumed by detritivores (II-H via 24 II-F, II-H) or decompose (arrow 34) to soluble materials that become a part of the dissolved mineral pool (II-D via 28 II-F, II-D). Detritivores and herbivores are each preyed upon by carnivores (II-I via arrows 23 and 25) and all three types of animals can become sources of detritus upon death [arrows 24 (II-H, II-F), 26, and 27].

102. While the major importance of the estuary with respect to the marsh includes tidal inundation and nutrient input (both dissolved and particulates) (arrow 35A), the major input of the marsh to the estuary is in the form of detritus and, to a lesser extent, dissolved minerals (arrow 35B). Exact contributions of marsh detritus to the total estuary detritus pool remain undefined, but the marsh contribution is large. An estimated net 3.08 metric tons/ha/yr of detritus is removed from the Georgia salt marshes (de la Cruz, 1971). Thus, the marshes play an important role in the contribution of this organic fertilizer to the estuaries by means of tidal transport (arrow 35B).

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* The exact origin of estuarine phytoplankton is controversial; while most algae can multiply in the water column, large contributions to the phytoplankton can be made by resuspension of organisms from the bottom of the estuary; i.e., they are either benthic or neritic forms. For a more thorough discussion, see Patrick, R. 1967.

PART IV: GENERAL OUTLINES OF MINERAL CYCLING AS
DESCRIBED BY THE GENERAL COMPARTMENTAL MODEL
OF THE MARSH-ESTUARINE ECOSYSTEM

Nutrient Cycles

Carbon cycle

103. The movement of carbon has been studied for many years in
both aquatic and terrestrial ecosystems (Odum, 1959; Woodwell and Pecan,
1973). Although carbon possesses several idiosyncrasies of its own,
its movement in the marsh-estuarine ecosystem does follow a trend
paralleling that found for this mineral in other ecosystems.

104. The general carbon cycle for any terrestrial or aquatic eco-
system may be described as follows. Primary producers (plants, algae)
fix inorganic carbon (carbon dioxide) taken from the atmosphere or from
water through the photosynthetic process to form organic compounds.
Some of the materials thus obtained are used by the primary producer
in biochemical maintenance (respiration), some are used for the forma-
tion of plant structural materials, and some are stored. Primary con-
sumers (herbivores) feed on the primary producers. While some material
is passed through the primary consumer gut unused, the remainder is as-
similated (converted to animal carbon) and used for maintenance (respira-
tion), the formation of various structural components, or is stored.
Secondary consumers (carnivores) consume primary consumers and use car-
bon thus obtained for their respiration, growth, and storage. Any orga-
nism not eaten by another organism will ultimately die and be consumed
by decomposer microorganisms. Decomposer microorganisms convert detri-
tus to CO_2 by way of their metabolic activity (respiration). The rate
of decomposition is dependent on the ambient environmental conditions
and the specific properties of the substrate being degraded.

105. The cycle of carbon dioxide in the marsh-estuarine ecosystem
is the same as that just described, except that the amount of marsh
grass material that dies and is decomposed by the microflora (arrow 12)
is large in relation to the amount of material consumed by the herbi-
vores (arrow 4). As a result, a large portion of the marsh-estuarine

carbon cycle is built around the utilization of decomposing grasses
(detritus). Detritus-feeding organisms (Detritivores, compartments I-F
and II-H) obtain their carbon by digesting the decomposer microflora
(compartments I-E2 and II-F2), the decomposition by-products sorbed to
detrital particles (compartments I-E1 and II-F1), and the entire detri-
tus particle itself. Carnivores then prey on the detritivores as well
as on the herbivores (arrows 7, 10, 23, and 25).

106. Table 2 presents some examples of production values attained
by members of each of the major biotic compartments in terms of carbon/
m^2/year. Values for detritus and the decomposer microflora are omitted
but will be considered in following sections. While there is a large
amount of variation even among the same species of primary producers
listed in Table 2, it is apparent that the primary producers as a group
have a greater productivity per unit area than do the consumers. What
is not apparent from Table 2 but would be evident from a more extensive
listing of primary producers is that marsh grasses attain production
values among the highest in any ecosystem. While the other rooted
macrophytes may approach the value obtained for grass production on a
per unit area basis, submerged, rooted macrophytes rarely encounter the
acres of optimal underwater area required to begin to rival the total
production values achieved by the marsh grasses (Woodwell et al., 1973).

107. Marsh grasses are the most significant primary producers in
the ecosystem. Approximately 10 percent of this production is consumed
by the marsh herbivores (arrow 4). The remaining 90 percent moves into
the detritus category (arrow 3) upon the death of the plant (Smalley,
1958). The rate and extent of detritus decomposition (arrow 12) varies
with many environmental factors and with the source of the detritus,
but values of 40 to 60 percent of new grass material added to the pool
per year are not uncommon (de la Cruz, 1965, 1973). The amount of de-
tritus consumed on the marsh by detritivores [arrow 9 (I-E, I-F)] has
not been determined. The rate of movement of detritus from marsh to
estuary (arrow 35B) is also poorly understood; estimates approaching
50 percent of the detritus produced per year have been obtained (Teal,
1962; Day et al., 1973; Banus et al., 1975). Values of 3.08 and 3.27

Table 2

Examples of Net Annual Production Rates for Each of the Major Marsh-Estuarine Compartments

Trophic Level, Compartment No. and Name	Representative Examples	Production Rates (g C:m^2:yr)*	Geographic Location	References
Primary producers				
I-B Marsh grasses	Spartina alterniflora	460**	Barataria Bay, La.	Kirby, 1971
		1153	Sapelo Island, Ga.	Odum and Fanning, 1973
	Juncus Roemerianus	503†	North Carolina	Waits, 1967
		628	Mississippi	de la Cruz and Gabriel, 1974
I-C Soil and epiphytic algae	Soil algae	32-40††	Delaware	Gallagher and Daiber, 1974
	Epiphytic algae	16††	Barataria Bay, La.	Day et al., 1973
II-C Periphyton and rooted macrophytes	Benthic algae	148	Barataria Bay, La.	Day et al., 1973
	Zostera marina (rooted macrophytes)	2200-4000‡	Rhode Island	Nixon and Oviatt, 1972
II-E Phytoplankton	Mixed populations	204††	Long Island Sound, N.Y.	Riley, 1956
		167	Barataria Bay, La.	Day et al., 1973
Primary consumers				
I-D Herbivores (marsh)				
Insects	Orchelimum	1.25 (adults)	Sapelo Island, Ga.	Smalley, 1958
	Micro-anthropods	0.12-0.14	North Carolina	McMahn et al., 1971
Snails	Littorina irrorata	10	Sapelo Island, Ga.	Smalley, 1958
	Average of Neritina reclivata, Melampus bidentita, Littorina irrorata	9.8	Barataria Bay, La.	Day et al., 1973
II-G Herbivores (estuarine)	Menhaden (Brevoortia patronus)	N/A	Lake Pontchartrain, La.	Darnell, 1961
	Striped mullet (Mugil cephalus)	N/A	Lake Pontchartrain, La.	Darnell, 1961
Secondary consumers				
I-G Carnivores (marsh)	Raccoons (Procyon lotor)	0.0084	Barataria Bay, La.	Day et al., 1973
II-I Carnivores (estuary)	Bay anchovy (Anchoa hepsetus)	N/A	Barataria Bay, La.	Day et al., 1973
	Bull shark (Carcharinus leucas)	N/A	Lake Pontchartrain, La.	Darnell, 1961
Detritus feeders				
I-F Detritivores (marsh)	Crabs (Uca pugnax, Sesarma)	3.1-12.2 / 4.8-7.4	Sapelo Island, Ga. / Sapelo Island, Ga.	Teal, 1958
II-H Detritivores (marsh)	Brown shrimp (Penaeus aztecus)	0-0.68725 (0.74 g organic matter:m^2:yr)	Barataria Bay, La.	Jacob and Loesch, 1971 Jacob and Loesch in Day et al., 1973
	Zooplankton (principally Acartia tonsa)	20 g organic matter:m^2:yr	Barataria Bay, La.	Day et al., 1973

* Underlined values are biomass in g dry weight/m^2 rather than gC:m^2:day or gC/m^2. These are given when no data are available for production. Productivity may be estimated by multiplying biomass by 2 in many cases (Day et al., 1973).
** Data obtained by taking 40 percent of the net annual production expressed as g dry weight:m^2:yr (Burkholder, 1956).
† Data obtained by taking 37 percent of the net annual production expressed as g dry weight:m^2:yr (de la Cruz, 1974).
†† Data obtained by dividing net annual production in g dry weight:m^2:yr by 2.5.
‡ This value is expressed as g dry weight:m^2:yr.

metric tons/ha/year have been quoted by de la Cruz (1971) for movement
of marsh grass detritus into Georgia estuaries and Mangrove detritus
into Everglades estuaries, respectively. According to de la Cruz (1973),
this corresponds to the 2-20 mg carbon/liter value for detritus found by
Odum and de la Cruz (1967) in water discharged from a Sapelo Island,
Georgia, tidal creek. The exact contribution of marsh grass detritus
to total estuarine detritus (compartment II-F) remains unquantified.
Current information does not permit differentiation between the dis-
charge of marsh production to estuaries in the form of particulate mat-
ter from the movement of production out of marshes and into estuaries in
the form of living organisms. Detrital material, whether of marsh or
estuarine origin, is primarily responsible for the murky quality of
water in many coastal bays and sounds (de la Cruz, 1973). The fact that
detritus is an important source of carbon for estuarine detritivores
[arrow 24 (II-F, II-H)] is somewhat better substantiated. Detritus con-
stitutes over 90 percent of the total seston in the estuary (de la Cruz,
1973). Zooplankton, such as Acartia tonsa, which would ordinarily ob-
tain the bulk of their nutrition from phytoplankton in less turbid
estuaries, have been observed feeding almost entirely on detritus as do
many benthic scavengers (Darnell, 1961). The carnivorous fishes that
depend upon estuaries as nursery grounds for their young depend heavily
on prey (compartment II-H) that obtain all or a substantial part of
their nutrition from detritus. While the exact carbon flow (or any
other nutrient) in this regime has not been quantified, it is felt that
a large percentage of the carbon that moves from the estuary to the
ocean (arrow 39B) is in packaged form as living organisms (Personal
Communication, May 1975, Armando A. de la Cruz, Professor, Department
of Zoology, Mississippi State University, Mississippi State, Miss.).

    108. The details covered by recent investigators have included the
amount of dissolved organic carbon released from standing dead marsh
grasses to tidal waters (arrow 35B) (Personal Communication, John Hall,
Microbiologist, University of Georgia Marine Institute, Sapelo Island,
Ga.; Personal Communication, John Gallagher, Plant Ecologist, University
of Georgia Marine Institute, Sapelo Island, Ga.), the amount of organic

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matter being produced by the roots of the various dominant marsh grasses [arrow 1 (I-B, I-A)] (Gallagher, 1974), and the dissolved organic carbon released by the decompositional processes occurring in the marsh soil (arrow 35B) (Pomeroy, 1975). The degree of detail is too complex for the present report.

Nitrogen cycle

109. The nitrogen cycle is very complex; however, it is also nearly complete because of the many self-regulating feedback mechanisms that are present (Odum, 1959). In addition, the nitrogen cycle relies heavily upon microbial processes. Microorganisms are responsible for the fixation of atmospheric nitrogen into forms usable by other organisms (ammonium, nitrate). Microorganisms also denitrify, i.e., convert nitrogen back into atmospheric nitrogen (see Alexander, 1961). Higher living organisms are basically parasitic rather than an essential feature of the cycle (Thimann, 1963). Although specific details of the biochemical rates and mechanisms are still being established, the general pathways of the nitrogen cycle have been known for quite some time (Odum, 1959; Alexander, 1961; and Thimann, 1963).

110. Molecular nitrogen in the air or dissolved in water is converted to organic nitrogen, ammonium, and nitrate by the nitrogen-fixing bacteria and algae. Nitrates and ammonium are taken up by the various primary producers and incorporated into the protoplasm and other cellular materials as organic nitrogen compounds. These compounds are then passed to the animals through the feed chain as described for carbon with appropriate changes from plant to animal compounds being made in the process. All dead organisms and the wastes of living organisms are subject to degradation by the decomposer microroganisms. As a result of their activities, the decomposers release various low-molecular weight nitrogenous compounds (amino acids, purines, pyrimidines, etc.). Included among the decomposers are the ammonifying bacteria that remove nitrogenous groups from the low-molecular weight compounds and release them to the environment in the form of ammonium. Ammonium can then either be taken up and incorporated by the primary producers, or it may be attacked by the nitrifying bacteria and oxidized first to nitrite

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and then to nitrate. Nitrate may also be used by the primary producers, or it may be taken up by denitrifying bacteria and reduced back to molecular nitrogen, thus completing the cycle.

111. Nitrogen enters the marsh-estuarine ecosystem by two different mechanisms. Molecular nitrogen may be fixed by the various microbial inhabitants of the marshes and estuaries. Although little or no fixation has been observed in the estuarine tidal water column (Whitney et al., 1975), rates up to $4x\ 10^{-3}$ µg $N:cm^2:hr$ have been observed in estuarine sediments (Brooks et al., 1971).* By contrast, approximately 100 µg $N:cm^2:hr$ was found to be fixed during early summer on the surfaces of salt marsh plots (Van Raalte et al., 1974). This amount was felt by the investigators concerned to be sufficient to account for the nitrogen contained in the maximum standing crops of grass in the plots (1.5 g N/m^2). Teal reports that he and his associates have found rates approaching 500 µg $N:cm^2:hr$ for bacterial fixation associated with Spartina roots and up to 250 µg $N:cm^2:hr$ for algal fixation on the marsh surface (averaged over a month); however, because of the larger coverage of grasses, bacterial fixation is an order of magnitude more important (Personal Communication, July 1977, John Teal, Ecologist, Woods Hole Oceanographic Institute, Woods Holes, Mass).

112. The alternate mechanism by which nitrogen enters the marsh-estuarine ecosystem is by transportation in river and tidal waters from the upstream watershed. Particulate nitrogenous compounds or other nitrogenous materials sorbed to the various suspended sediments may be carried into the estuary. These may then be deposited on the marsh surface by the tides. However, no data are available on the amount of nitrogen transported in this manner. Nitrogen may also be brought into the estuary in solution by the incoming streams and subsequently carried into the marsh by the tides. Deposition of particulate-bound nitrogen is an important fertilization mechanism for the marsh grasses in well-established areas (Teal and Teal, 1969). Dissolved nitrogen is probably more important to marsh grasses in newly established areas where

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* Computed from the 37 µg $N:cm^2:yr$ value given by Brooks et al. (1971).

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sandy soil permits easy penetration of the fertile tidal waters. While
no data are available for the nitrate or ammonium concentrations of
flood or ebb tide waters, Ho and Lane (1973) hypothesized that the
waters moving up onto the marshes will have a higher nitrate content
while those waters departing the marsh will have more ammonium, primar-
ily as a result of exchanges with interstitial water in the marsh soil
and the estuarine sediments near the marsh. The estuaries themselves
have the requisite microflora to carry out nitrification of ammonium
and, indeed, this process has been measured in the Scheldt Estuary in
Belgium (Billen, 1974). The marsh surfaces are actually optimized for
the removal of nitrogen by the denitrification process, having an aero-
bic surface layer overlying an anaerobic lower layer (Engler and Patrick,
1974; Engler et al., 1976).

113. Within the marsh itself, nitrogen appears to be a limiting
factor for primary production as is the case with the adjacent coastal
waters (Ryther and Dunstan, 1971). Several investigators have reported
that the addition of fertilizers containing nitrogen to marsh plot sur-
faces stimulated the growth of marsh grasses, whereas the addition of
phosphorus-containing fertilizer did not (Sullivan and Daiber, 1974;
Gallagher, 1975a; Patrick and Delaune, 1975). Relative to carbon, the
actual nitrogen content of the marsh grasses is very low. For example,
on a percent dry weight basis, Spartina alterniflora contains 40.77 per-
cent carbon, but only 2.12 percent nitrogen (Burkholder, 1956). Juncus
roemerianus contains even less nitrogen with its readings being 36.60
percent carbon and 0.46 percent nitrogen (de la Cruz and Gabriel, 1974).
Brannon (1973) showed that nitrogen content varies seasonally in
Spartina alterniflora in southern Louisiana and averages 2.8 percent.
It is apparent that the nitrogen contents of the marsh grasses, which
form the bulk of the detritus, cause the vegetative component entering
the detritus-microbial decomposer compartment (compartment I-E) to be
nitrogen-poor.

114. While the flow rate of nitrogen from detritus to detritivore
has not been measured, it is evident from the preceding documentation
that detritus is a reasonably good source of organic nitrogen for the

detritivores and, therefore, the detritus-based food chain. The exact
function of the marsh-estuarine ecosystem relative to nitrogen cycling
has not been completely defined, but the tendency of some investigators
is to look upon this ecosystem as a sink rather than a source of nitro-
gen, at least for the southeastern United States coastal area (Haines,
1975). Incoming fresh water (arrow 36) does contain substantial levels
of nitrogen, especially as nitrate; however, by the time the freshwater
input has reached coastal waters, it has been relatively depleted of
nitrogen (Haines, 1975). By contrast recent data of Teal and Valiela
(In press) and Valiela et al. (Report in preparation) show very large
exports of nitrogen (Personal Communication, June 1977, Ivan Valiela,
Associate Professor, Boston University Marine Program, Marine Biological
Laboratory, Woods Hole, Mass.).

Phosphorus cycle

115. The intricacies of the phosphorus cycle are far less complex
than those of the nitrogen cycle. Yet, because phosphorus has its
source and sink in the lithosphere rather than in the atmosphere, "the
phosphorus cycle is far more elusive than the nitrogen cycle and needs
more definition for field personnel." Much of the phosphorus not ac-
tively tied up in living protoplasm tends to be returned to the
lithosphere.

116. The majority of the phosphorus compounds in the lithosphere
exist as inorganic phosphate (Odum, 1959; Alexander, 1961). Erosion of
phosphate-bearing rocks releases phosphorus to the surrounding environ-
ment as dissolved phosphate borne in the various waters. Dissolved in-
organic phosphate is taken up by primary producers and microorganisms.
From here it may be passed up the food chain as organic phosphates.
Organic phosphate can be excreted back into the dissolved phosphate pool
by any member of the food chain, including the primary producers them-
selves. Phosphate retained within the biota is released by autolysis
or upon death by the activities of the decomposer microflora organisms,
unless that phosphate has been bound up in such poorly decomposable
structures as bones and teeth. Much of the dissolved phosphate finally
ends up in the sea where it may be deposited in shallow sediments or

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lost to deep sediments. Barring geologic uplift, materials bound in deep sediments stand a rare chance of being placed into circulation again (Odum, 1959).

117. Phosphorus enters the salt marsh-estuarine ecosystem by the same transport mechanisms as nitrogen. Fresh water entering the estuary from the watershed carries phosphate into the estuary in both particulate and dissolved form (arrow 36). Input levels of dissolved phosphate into estuaries range from 1 to 10 μg-atoms/ℓ as phosphate-phosphorus (Ketchum, 1969; Hobbie et al., 1975). However, no information is available on the amount of particulate phosphorus entering estuaries. The range of dissolved phosphorus concentrations in the brackish water zones seems to be within 1.20 to 3.0 μg/ℓ as phosphate-phosphorus (compartment II-D) (Pomeroy et al., 1965; Ketchum, 1967).

118. The phosphorus requirements of marsh-estuarine vascular plants, both submerged and intertidal, seem to be met in much the same manner. Eelgrasses (Zostera sp., compartment II-C) obtain their phosphates by pumping them up from the sediments (McRoy and Barsdate, 1970). An amount more than sufficient to meet the demands of the plant is obtained. Consequently, excess phosphates are excreted into the surrounding sea water [arrow 16 (II-C, II-D)] (McRoy and Barsdate, 1970). Similar results were found for the marsh grass Spartina alterniflora by Reimold (1972). He found that this plant can take up phosphate from as deep as 100 cm within the marsh soil [arrow 1 (I-A, I-B)]. Excess phosphates were found to be excreted onto the surfaces of the marsh leaves and removed from there by tidal waters at high tides (arrow 35B).

119. The phosphorus content of marsh grasses (compartment I-B), like that of nitrogen, is very low relative to carbon. For example, while Spartina alterniflora contains 40.77 percent carbon, the phosphorus value is only 0.25 percent (Burkholder, 1956). Juncus roemerianus, which has a carbon content of 36.60 percent, possesses 0.24 percent phosphorus (de la Cruz, 1973). While such values are low, the actual phosphate levels available to the marsh grasses do not seem to be limiting to their growth (Gallagher, 1975a; Patrick and Delaune, 1975). The concentration of phosphorus in algal cells (compartment I-C)

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generally seems to run between 10^{-8} and 10^{-6} µg P/cell (Franzew, 1932; Lund, 1950; Goldberg et al., 1951; Mackereth, 1953; and Al Kholy, 1956).

120. Information on the phosphorus contents of marsh soil (compartment I-A) is generally unavailable in the literature. Ranwell (1972) found phosphorus levels from 0.07 to 0.11 percent of oven-dry weight of newly accreted silt in a Spartina anglica marsh (England). Chabreck (1972) examined the coastal soils of Louisiana. He found that the average phosphorus contents of soils of the saline vegetative type was 0.08 ppt (g P/g of soil) with a range of 0.06 to 0.13 ppt. By contrast, the same investigation was done on soils of the brackish vegetative type and yielded an average of 0.04 ppt of phosphorus within a range of 0.01 to 0.10 ppt (Chabreck, 1972). A study done on Pamlico Estuary sediments (compartment II-B) yielded much lower values ranging from 1.6 ppb (µg P/g of sediment) in fresh water to 0.3 ppb in brackish water (Upchurch et al., 1974). However, the exchange values between estuarine sediments and water seem to be rather high with sediments releasing phosphate to the water when water is low in initial phosphate levels (below 1 µg/ℓ); however, when water is high in initial phosphate (greater than 1 µg PO_4/ℓ), sediment tends to take up excess phosphate (Pomeroy et al., 1965).

121. Phytoplankton in the estuary (compartment II-E) both take up and release phosphorus. Although the uptake form [arrow 18 (II-D, II-E)] is inorganic phosphate, the release [arrow 18 (II-E, II-D)] seems to occur in the organic form (Coffin et al., 1949; Ketchum and Corwin, 1965; Satomi and Pomeroy, 1965; and Ketchum, 1967). Generally, phosphorus would not seem to be limiting to phytoplankton at the concentrations usually found in estuarine waters. Phosphorus is one of the most dynamic of the major biological elements, and many organisms assist in its turnover (Pomeroy et al., 1963; Johannes, 1965; Lean, 1973; and Peters and Rigler, 1973). Turnover times reported for inorganic phosphate in the literature are remarkably rapid, varying from 1 hr in an algal bloom in an estuary to 34 hr in coastal water during daylight hours (Pomeroy, 1963).

122. Whether the marsh-estuarine ecosystems serve as traps for

phosphorus moving through them or tend to release phosphorus to water moving out to the coastal waters remains somewhat controversial (Haines, 1975; Hobbie et al., 1975). The lack of a biological phosphorus limitation in coastal waters obtained from fresh waters that have moved through the marsh-estuarine ecosystem strongly suggests that at least a nonlimiting level of phosphorus is reaching the coastal waters (Haines, 1975).

Sulfur cycle

123. Although the cycling of sulfur has been well studied in terrestrial ecosystems and is currently receiving much attention in freshwater watersheds, very little attention or research has been focused upon sulfur in the marsh-estuarine ecosystem. Despite this fact, sulfur is an important nutrient for biological systems, especially as a component of the amino acids cystine and cysteine (White et al., 1964). However, too much sulfur can, in the proper chemical form, be quite lethal.

124. The cycle of sulfur is complex and involves many reactions and oxidation states. The availability of this material is strongly influenced by biogeochemical processes. Sulfur is taken up from the environment by the primary producers as sulfate and from here it is reduced and combined with carbon materials as organic sulfur. Organic sulfur may be passed along the food chain in normal fashion or eliminated as a waste material along the way. Organic sulfur in waste products or dead organisms is released first as free organic sulfide, then oxidized to thiosulfate, polythionates, sulfur, polysulfurs, and sulfate. The forms present are dependent upon whether the environment is anaerobic or aerobic, and the amounts vary rapidly in time and space. The inorganic forms of sulfate or sulfide are further subject to reduction or oxidation, depending upon the environment and the nature of the biota present. Both sulfate and sulfide are capable of forming insoluble complexes with inorganic cations such as barium or with heavy metals.

125. In the salt marsh-estuarine ecosystem, the form of sulfur depends upon the part of the ecosystem being considered. The anaerobic environments of the salt marsh soil (compartment I-A), tidal flats, and estuarine sediments (compartment II-B) contain primarily sulfide while

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the oxygenated water of the estuary (compartment II-A) contains predominantly sulfate (Ramm and Bella, 1974). While the biota contain organic sulfur compounds, the specific form and amount has not been studied nor have the pathways of sulfur circulation in the estuary been examined. Thus, the exact pathways of sulfur movement are unknown. It is assumed that since the sulfate concentration in fresh water is much lower than in the sea water or brackish estuarine water, the sulfate in estuarine water is imported primarily from the sea (arrow 39A). Sulfate imported into the marshes with the tides (arrow 35A) percolates into the anaerobic zone of the marsh soil where it is reduced to sulfide. Reoxidation of sulfide to sulfate is possible wherever oxygen is able to diffuse out of the marsh grass roots [arrow 1 (I-B, I-A)].

126. Oxidation of sulfides can create a problem in the marsh soil wherever conditions become sufficiently oxidizing to permit conversion of large amounts of sulfide to sulfate. For example, when sulfide-laden reduced bottom sediments are deposited on the marsh surface above tide level or when marshes are drained, the marsh soil becomes aerobic. In addition to the large amounts of heavy metals (mainly iron) mobilized by conversion of insoluble metal sulfides to more soluble metal sulfates, the acid activity of the resulting sulfuric acid results in formation of poor cat clay soil, which is unsuitable for marsh grasses or any other type of vegetation.

Heavy Metal Cycles

General

127. The heavy metals cadmium, copper, iron, mercury, manganese, nickel, lead, and zinc will be considered in one general section rather than being discussed individually. There are several reasons for this. First, a complete in-depth knowledge of the details involved in the cycling of many of these metals is lacking, although a general understanding of each is available. For example, Wong et al. (1975) have recently discovered that lead can be biologically methylated under circumstances that are environmentally similar to those that favor the

biological methylation of mercury. However, no ecological importance has been found for lead methylation in situ.

128. Second, the knowledge of the behavior of heavy metals within entire ecosystems and particularly in marsh-estuarine ecosystems is unclear. While some of this vagueness results from an incomplete knowledge of the biogeochemistry of individual metals, a good portion of the problem results from the particular "focus" of research on marsh-estuarine ecology. Windom (1975) has observed that much of the research on these ecosystems has been confined to those interactions that occur at river-estuary boundaries. Particular examples of this type of work include the efforts of Kharkar el at. (1968), Turekian (1971), and Windom et al. (1971). Such work has been aimed at determining the qualitative and quantitative characteristics of the heavy metal load borne by riverine systems and has also been concerned with the characteristics of the heavy metals that are finally delivered to the ocean. Additional research has been concerned with the function of the marsh grass Spartina alterniflora in regulation of the mobilization of iron and zinc (Pomeroy et al., 1969; Williams and Murdock, 1969; and Bhate, 1972), copper, cobalt, iron, manganese (Bhate, 1972), and mercury (Rhan, 1973). However, few studies have been sufficiently large in scope to contend with the net flux of metals through marsh-estuarine ecosystems or even between marshes and estuaries. Exemplary works in this area include those of Rhan (1973), Banus et al. (1974), Banus et al. (1975), and Dunstan et al. (1975) on salt marshes, the treatise of Mathis (1973) on mangroves and estuaries, the effort of Drifmeyer and Odum (1974) on dredge material pond ecosystems, and the endeavors of Holmes et al. (1974) and Windom (1975) on marine and salt marsh ecosystems.

129. A final reason for combining all of the metals in one discussion is that much of the work that has been done to date indicates that many metals move through the estuary following similar patterns since the processes that influence the mobilization or sedimentation of these materials are often the same.

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Processes governing
movement of heavy metals

130. There are several general processes that can be distinguished
as playing a major role in governing the movement of heavy metals
through salt marsh-estuarine ecosystems. Carpenter et al. (1975) have
enumerated several principal mechanisms involved in determining the
final concentration of a given heavy metal in estuarine waters. They
include:

    a. Physical flow and mixing activities occurring between
        waters of riverine and marine origins.

    b. Primary biogenic reactions--processes concerned with the
        uptake and release mechanisms of living and detritus
        particles and with the genesis and decomposition of new
        compounds.

    c. Secondary biogenic reactions--mechanisms involved in
        determination of hydrogen ion concentrations and redox
        equilibria.

    d. Physical-chemical reactions--processes resulting in
        changes of equilibria due to changes in temperature or
        nonspecific ion interactions and ion exchanges between
        water and solid materials.

131. The specific physical-chemical reactions predominating at the
actual boundaries of the river-estuary and marsh-estuarine soil have
been discussed in detail by Windom (1975) and include adsorption-
desorption reactions, flocculation, precipitation, and sedimentation.

132. Several important biological processes permit the biota of
marsh-estuarine ecosystems to play a key role in the regeneration and
movement of heavy metals within the ecosystem. The uptake of heavy
metals from marsh soils by marsh grasses [arrow 1 (I-A, I-B)] has been
observed and measured by several investigators, including Banus et al.
(1974), Dunstan and Windom (1975), Banus et al. (1975), Drifmeyer and
Odum (1974), and Dunstan et al. (1975). Presumably, rooted aquatic
macrophytes are also capable of extracting heavy metals from estuarine
sediments [arrow 15 (II-B, II-C)]; however, this possibility has not
been examined. Planktonic algal species can concentrate some metals,
especially organic forms of mercury [arrow 18 (II-D, II-E)] (Matsumura
et al., 1971). Biological methylation of heavy metals in

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marsh-estuarine ecosystems has not been extensively studied. However, the requisite environmental conditions for methylation are present in estuaries, so the process can be important as dramatized by the Minimata Bay catastrophe in Japan (Ratkowsky et al., 1975). The concentration of heavy metals in detritus-based biological food chains following uptake from marsh soil by marsh grasses has been studied only to a very limited extent. The results obtained to date do indicate a movement of metals into detritivorous forms such as mussels, crabs, and shrimp [arrow 9 (I-E, I-F)] (Drifmeyer and Odum, 1974; Banus et al., 1975). A final form of biological participation in the movement of heavy metals through the salt marsh-estuarine ecosystem involves the products of biological decomposition. Organic particulates (detritus) can sorb metals, particularly mercury (arrow 28) (Rahn, 1973). Consequently, metals subject to binding by these organics can be concentrated in detritivore-based food webs. The metals may also be scavenged from water by the sorptive processes [arrow 28 (II-D, II-F)] and subsequently removed entirely when the host particles settle to the bottom of the estuary (arrow 33d). In addition, the soluble organic products of decompositional processes, particularly humic acids resulting from degradation of marsh grasses and algae, are well known for their ability to chelate and hold heavy metals in aqueous solution [arrow 28 (II-F, II-D)] (Schnitzer, 1971). Zinc is a particularly good example of a metal involved in this process (Carpenter et al., 1975).

Outline of metal flux
through the ecosystem

133. While no one metal is guaranteed to follow a given pathway during its passage through the salt marsh estuary, a set of general trends can be outlined that describe average tendencies for heavy metals (marked individual variations from these trends will be enumerated). In the following outline modified from the description of Windom (1975), it is assumed that the metals are moving into the marsh estuarine ecosystem primarily in freshwater input from rivers. However, in certain cases, alternate sources of input such as the atmosphere can place considerable levels of a metal into the ecosystem. Lead is an outstanding

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example wherein atmospheric input to the salt marsh may actually exceed the input brought in by the rivers on the tides (Banus et al., 1975).

134. The processes of mixing, adsorption-desorption, flocculation, precipitation, and sedimentation occurring at the river-estuary boundary delimit both the form and the rate of metal input into the estuary. Once into estuarine waters, metals may be removed from the water by precipitation and sedimentation [arrow 17 (II-D, II-B)]. By contrast, those metals that have been built up in estuarine sediments by depositional processes can be remobilized by biological activity and/or chemical interactions with the water column [arrow 17 (II-B, II-D)]. The mobilization and precipitation-sedimentation processes acting in concert with estuarine circulation patterns then serve as determinants of the residence times for metals within the waters of salt marsh-estuarine ecosystems. In addition, the large accumulation of organic particulates (detritus) in the water and sediments of the salt marsh-estuary tend to sorb and remove metals from the water [arrow 28 (II-D, II-F)]. Sorption and removal act in unison with the generally high concentrations of precipitate-forming sulfides present in marsh-estuarine waters to further decrease the residence times for waterborne metals and cause the salt marsh-estuarine ecosystem to generally act as a sink for many metals entering the system. Opposing the metal scavenging and removal mechanisms just enumerated are the intense biological processes of salt marsh-estuaries that tend to recycle metals that would otherwise be locked up within estuarine sediments and marsh soils. This is exemplified by the appearance of maximal concentrations of many metals in soluble form in late fall and winter corresponding to the time of maximum decay of vegetation in the watershed and marsh (Carpenter et al., 1975). However, the fact remains that few metals in a noncomplexed, inorganic, ionic state can freely move through the estuary and out into the open ocean.

135. Once in coastal and oceanic waters, heavy metals are besieged with numerous flocculation, precipitation, sorption, and dilution processes, which serve to lower their relative abundances in water (Windom, 1975).

Fates of individual heavy metals

136. Both iron and manganese, the metals brought into estuaries
by rivers in the highest concentrations, suffer a similar fate. As a
result of the formation of insoluble phosphates, virtually all iron pre-
cipitates upon entry into the estuary (via arrow 35A) and much of this
precipitate accumulates in salt marsh soils (Windom, 1975). Manganese
also forms insoluble phosphate complexes that precipitate out upon entry
into the estuary. The net flux from the estuary into the ocean is much
less than the dissolved input by rivers (Windom, 1975). However, in one
instance, manganese was found to be released from Chespeake Bay sediments
during the summer months when the pH and dissolved oxygen levels de-
clined in the waters at the bottom of the estuary (Carpenter et al.,
1975).

137. Copper and cadmium in dissolved, but uncomplexed, inorganic,
ionic form do not tend to form insoluble precipitates by combination
with other inorganic compounds. Therefore, these metals are able to
move through estuaries relatively untouched by those processes that
serve to remove other metals. However, these metals have a large affin-
ity for organic humates and are readily complexed by these materials.
Thus, almost all of these metals entering the estuaries attached to
particulates can be recovered from the estuarine sediments, also in
particulate form (Windom, 1975).

138. Mercury is desorbed from the particulate phases with which
it is associated upon exposure to saline conditions [arrow 28 (II-F,
II-D)]. Consequently, the amount of this metal in solution in the
estuary tends to increase over the dissolved levels entering the estuary
in fresh water (Harriss et al., 1971; Windom et al., 1971). Mercury
is also actively concentrated from salt marsh soils by _Spartina_ _alterni-_
flora resulting in high concentrations of mercury in plant material.
The plant material is largely retained by the marsh soil [arrow 1 (I-B,
I-A)], because most of the mercury remains within the plant roots
(Harriss et al., 1971; Rahn, 1973; and Windom, 1975). Overall, most of
the total mercury entering the ecosystem is transported to the oceans
with a small amount being trapped and retained within the system (Windom,
1975).

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139.   Lead is apparently not precipitated by the chemical inter-
actions occurring during the transition from river to estuarine water.
However, the dissolved levels of this metal entering the estuary under
natural conditions are low (1-5 ppb) (Windom, 1975). Large levels of
lead do enter the estuary in particulate form, however, and these are
rapidly sedimented either upon the marsh surface or in the estuary
(arrow 33d) (Windom, 1975). Spartina plants do accumulate lead in na-
ture (Banus et al., 1974; Windom, 1975). However, between the formation
of highly insoluble lead sulfides [arrow 28 (II-F, II-D)] and the sedi-
mentation of lead bound in organic detritus (arrow 33d), little lead
probably leaves the estuary.

140.   Zinc, next to iron, is the most biologically active of the
metals considered. While zinc is supplied to the estuary in both dis-
solved and particulate form, the mixing processes govern the variations
in both the extractable and bound forms associated with the particulate
zinc. However, in the subsurface (saline) waters of the estuary, the
desorption processes active on both extractable and bound zinc in sus-
pended sediments predominate [arrow 28 (II-F, II-D)]. Evidently the
zinc is actively cycled between the sediments and the water. During the
productive months when zinc levels are at their maximum in the salt
marsh estuary, the soluble zinc is predominant in organic complexes of
biological origin (Carpenter et al., 1975; Fukai et al., 1975). While
the amount of zinc moving through the estuary has not been assessed,
there is probably a net flux outward into the sea as a result of zinc's
tendency to remain in solution through biological activity. Zinc is a
necessary micronutrient for many biological processes. As a result,
zinc is retained in the biota often by complexation with organic
compounds.

PART V: SUMMARY AND CONCLUSIONS

Summary

141. Marsh-estuarine ecosystems possess intrinsic properties,
which render them valuable to both man and nature. The state of the art
of present knowledge of the ecosystems has not reached the point that
permits answer to the question, "How much is the fertility of the estu-
arine and coastal waters decreased every time 1 ha of marsh is taken out
of production?" (de la Cruz, 1973). However, recognition of the value
of marsh-estuarine ecosystems is increasing. A portion of the diffi-
culty in assessment of the value of marshes arises from an inability to
assign an exact monetary value to each of the many aspects of marsh
ecology.* Another problem in assignment of values to marshes results
from the fact that much of the "cash value" of marsh-estuarine ecosys-
tems is harvested upriver from the estuary and, more importantly, in non-
estuarine coastal waters.

142. The following values are recognized as definite worths of
marsh-estuarine ecosystems, even if difficulty is experienced in place-
ment of exact dollar values on them. Marshes and estuaries function as
one integrated ecosystem. Marshes are totally dependent upon estuaries
for both their origins and for their continued existence (maintenance).
On the other hand, between 19 and 29 percent of the organic matter in an
estuary is organic detritus that has its origins in the marshes that
surround it (Heimle and Flemer, 1976). Both the marsh and the estuary
export biological production and also mineral and organic nutrients that
can support biological production. Much of this manifests itself as
living production that is harvested by coastal fisheries. As a food
source, spawning ground, and shelter for juveniles of many marine spe-
cies, the marsh-estuarine ecosystem serves as a nursery for valuable
coastal fisheries. Physical shelter is provided not only in the grassy
tidal marshes but also by other estuarine-based communities, including

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* For an attempt at this, see Gosselink et al., 1973.

mangroves and seaweed and sea grass beds.

143. Marsh-estuarine ecosystems are of benefit to man in the buffer value they provide coastal areas from marine storms. These ecosystems absorb the energy of incoming tidal storm waves and also soak up coastal storm waters resulting in decreased damage to inland areas. An unrecognized marsh-estuarine function of potentially considerable economic importance to the Corps of Engineers is the silt-absorbing capacity of developing salt marshes that operates in conjunction with the "clearing capacity" of large excursions of tidal waters into and out of estuaries and consequently tends to keep harbors and basins in estuaries free of navigation-impeding sediments. The former mechanism operates to keep silt introduced into the estuary from filling in the channel, while the latter process tends to automatically "dredge" sediments from important central passages (Gosselink et al., 1973).

144. The grazing food chain includes algae and vascular plants as the dominant primary producers. Algae occur both as phytoplankton and as periphyton. The algae are predominantly grazed by herbivorous zooplankton and benthic invertebrates. Lower carnivores then prey on herbivorous species. Top carnivores prey on lower carnivores and on herbivores. In the second or detritus-based food chain, marsh grasses and algae, rather than being utilized directly, die and are consumed by microbial decomposers. Microbial decomposers are composed of the bacteria and fungi that actively degrade vegetative and animal tissues and the protozoans that graze upon the bacteria. Detritivores, largely invertebrates, feed on dead and undecomposed plant materials as well as the decomposed ones, deriving their nutrition mainly from the microbial decomposers, decomposition products of microbial decomposers, and also from low molecular weight organic products associated with dead vegetation, animal remains, and fecal materials. Detritivores form the food source for the lower carnivores, while the higher carnivores prey on both the lower carnivore and the detritivore populations.

145. Some estuaries lack the extensive marshes that generate the large detritus loadings that produce turbidity and shade out phytoplankton. The water of such estuaries is often dominated by phytoplankton

blooms, or the water may be relatively clear of any particulates. Estuaries having any degree of turbidity will have a fauna more strongly oriented toward the detritivore food web. Detritivore food webs tend to dominate most eastern and southeastern Atlantic and all Gulf Coast estuaries plus some West Coast marsh-estuarine ecosystems.

146. Marsh-estuarine ecosystems play important roles in mineral cycling. The reduction of carbon from the inorganic to the organic state can occur elsewhere, but it seldom occurs with the intensity found in the salt marshes. It is the intensive production of organic material in the form of plants that makes the marsh-estuarine ecosystem so valuable to fish and shellfish industries. While the net export of carbon to the oceans in dissolved or nonliving particulate form has not been thoroughly established, the production in the marsh-estuary of living organisms followed by migration of these organisms from the estuary to the ocean is well recognized. These migrating organisms may be directly usable in themselves or may serve as food for other forms. The net movement of carbon from the marsh to the estuary has been well established and is vital to the function of the estuary as a nursery.

147. The close proximity of oxidizing and reducing environments as found in salt marsh soils and many estuarine sediments is a prerequisite for the completion of the biogeochemical cycles of nitrogen and sulfur. In the case of nitrogen, the denitrification processes require an extremely intimate relationship between oxidized and reduced zones in order to permit the aerobic oxidation of ammonium to nitrate followed by the anaerobic reduction of nitrate to molecular nitrogen. In the case of sulfur, reduction of sulfate to elemental sulfur and sulfide also requires anaerobic muds for the sulfate-reducing microorganisms to conduct their activities. Again, tidal marsh soil and estuarine sediments play a key role and the marsh-estuarine ecosystem appears to be a sink for both nitrogen and sulfur.

148. While phosphorus does move out through the marsh-estuarine ecosystem and into coastal waters, the marsh-estuarine system does serve to regulate phosphorus release. In the case of the closely studied coastal Georgia marsh-estuarine ecosystem, the efficiency of the

phosphorus regulation mechanism is so effective that despite wide ranges
of the input by incoming river waters, the concentration of phosphorus
within estuarine waters varies little during the year. This is princi-
pally a result of the uptake and release mechanisms between the estu-
arine sediment and marsh soil elements with the estuarine water. Thus,
while there is a steady phosphate input to the coastal waters, the marsh-
estuarine ecosystem acts as a filter to dampen extreme releases and also
to prevent phosphorus impoverishment of water.

149. While copper, cadmium, and lead in ionic, inorganic, dis-
solved form move through the system easily, zinc and mercury also manage
to get to the sea, although the later metals require more time to do so.
The marsh-estuarine ecosystem is a sink for the metals iron and manga-
nese and for particulate copper, cadmium, and lead. This ecosystem is
both dynamic and complex in its handling of metals. While many forces
act to sediment, sorb, or precipitate the metals from solution, others
tend to strip metal from particulates or otherwise act to dissolve
metals and bring them into solution. The intensive biological activi-
ties occurring in this ecosystem also have a tendency to mobilize metals.
The major process involved in this includes direct uptake from soils and
sediments by plants. This is followed by release of metals to other
members of the biota upon consumption of plant materials or by release
of metals to the environment as a result of decomposition processes.
Metals may also enter the food chain by sorption onto surfaces of food
(usually detritus) followed by ingestion and incorporation. Alterna-
tively, metals may enter the biota after complexation by organic prod-
ucts of biological origin followed by sorption of the organics onto in-
organic particulates that are subsequently ingested.

Conclusions

150. There is no set criteria for essessment of what constitute
ecologically necessary marshes. While "current" technology does not
give a good handle on the exact or even the general value of each acre
of marsh, the destruction of marshes for any purpose is environmentally

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unsound and should be discouraged. Techniques for marsh development are either available or in the process of development, but it is doubtful if a one-to-one "marsh created" for "marsh destroyed" policy will ever be feasible. With energy considerations entering the picture, marsh development will probably represent an even less favorable prospect, except where the development process can occur in the immediate proximity of the dredging.

151. The physical act of dredging estuarine sediments does relatively little harm to the marsh-estuarine ecosystem except for destroying or disrupting those organisms unfortunate enough to be in the dredging area. However, problems may arise with the smothering or displacing of organisms in the discharge area. Another problem can come about when dredged materials are deposited on the marsh surface. In addition to smothering marsh organisms, dredging may elevate the marsh beyond permissible boundaries for marsh development. Once the dredged material is deposited on the marsh surface, the forces of tides, wind, and storm may erode the materials into the estuary before any plant species can colonize them.

152. Chemical release of minerals from dredged materials into the environment has the potential to cause several problems. When intensely contaminated materials are removed from an anaerobic zone in the estuary to an aerobic one (marsh or estuary), problems can arise both from the oxygen demand exerted by the reduced compounds in the dredged material and from any heavy metals and sulfides contained in the material. These minerals can assume more mobile forms after oxidation. When used on marsh surfaces, sulfide-laden dredged materials can lead to marsh infertility resulting from metal toxicity and cat clay formation.

153. Release of nutrients resulting from the use of nutrient-rich dredged materials for marsh creation could cause other difficulties. Nitrogen-rich sediments will stimulate the growth of marsh grasses. In an estuary having low dissolved oxygen levels, the additional oxygen demand created by extra detritus in the water column could further deplete the oxygen concentrations and cause problems. Additional nitrogen and phosphorus released into the estuary by marsh soils would probably

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not create difficulties since the inherent light limitations present in most estuaries would prevent excessive plant growth. When this is coupled with the fact that most estuaries are adapted to nutrient-rich (eutrophic) schemes, the problem appears potentially insignificant in most cases. Excessive organic carbon in sediments used for marsh creation could cause difficulties; materials escaping the marsh would tend to increase the BOD loading of the estuary with resulting oxygen depletion problems. A sediment that contains high levels of both nutrients and heavy metals could cause problems for marsh development; the excessive growth stimulated by nutrients will prompt the uptake of heavy metals by marsh grasses at rates and concentrations far in excess of normal (Banus et al., 1975). Such a volume of heavy metals, if not toxic to marsh grasses during growth, would constitute a slug load to the detritivore population at the end of the growing season. Present knowledge of marsh-estuarine ecology is inadequate to permit to assessment of the impact of this loading. Until more is known, it is recommended that the use of dredged materials containing nutrient or heavy metal levels in excess of those existing in natural marsh soils of the area should be avoided.

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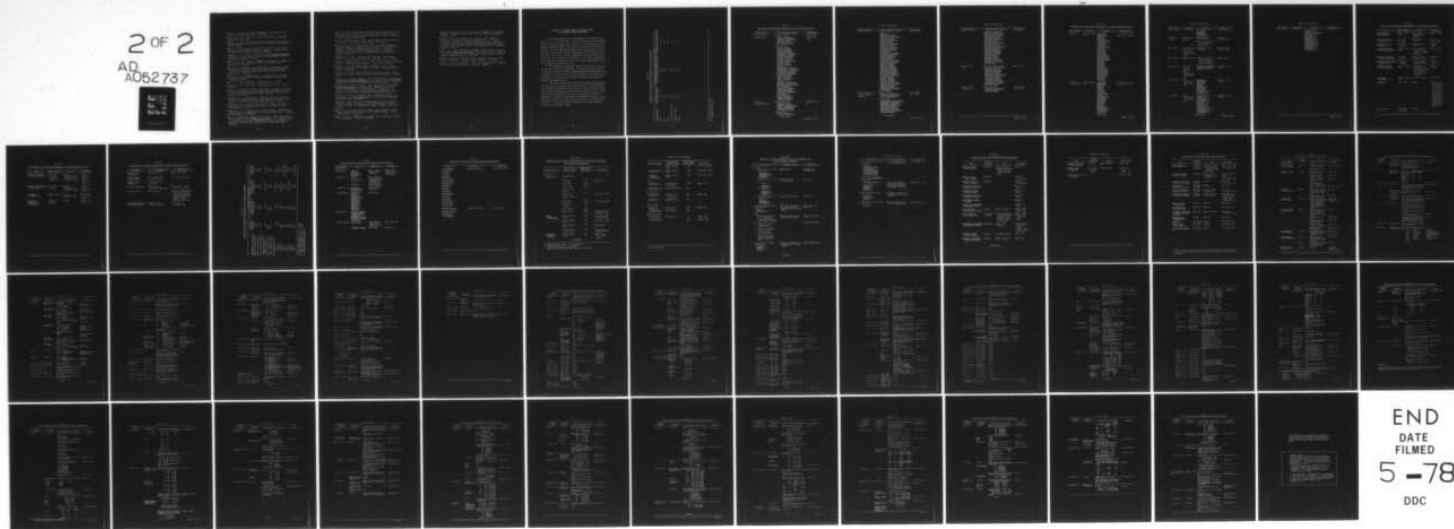
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APPENDIX A: SUMMARY TABLES FOR GENERAL MODEL
OF THE MARSH-ESTUARINE ECOSYSTEM

1. The tables contained in the Appendix are an extension of Ta-
bles 1 and 2 in the main volume. Tables A1 through A13 of the Appendix
present a detailed listing of the contents of each compartment in the
general compartment model. Where possible, geographic occurrences are
specified for each compartmental member listed in the tables. No de-
tails are presented for estuarine compartment II-D, the dissolved min-
eral pool. The contents of this compartment are described within the
tables that list nutrients and heavy metals. All tables contained in
the Appendix are intended for use with the general compartmental model
in the same manner as Tables 1 and 2.

2. The information contained in Tables A1 through A22 is for use
as reference material. Consequently, no discussion has been made of
the materials contained in them. Appendix Tables A14 through A22 give
listings of the current state of the art knowledge of the forms, rates,
and amounts of nutrients and heavy metals cycled as depicted by the
general compartmental model.

3. Any person desiring more detailed information than that given
in the tables may easily find the original source of the information
by consulting the Literature Cited section of the main volume. Where
very limited information was available for the construction of a given
table describing mineral cycling, only the available information is
presented. For example, presentation of information for arrow 1 fol-
lowed by information on arrow 5 indicates little or no information for
arrows 2-4. This avoids needless repetition of "No Data Available"
as found in more complete tables.

Table A1

Composition of Salt Marsh Compartment I-A, Salt Marsh Soil

Constituent	Occurrence in Salt Marsh Soils, Percent		
	Gulf Coast (Fla.)*	S. E. Atlantic Coast (S. C.)*	Atlantic Coast (N. C.)**
Sand	74.0	25.6	97.3
Silt	14.0	59.2	0.6
Clay	2.0	4.0	2.1
Colloidal material	10.0	11.2	--
Organic matter	12.6	13.4	0.1
CaCO₃	7.0	8.2	--

* Kurz and Wagner, 1957
** Broome et al., 1973

Table A2

Composition of Salt Marsh Compartment I-B, Salt Marsh Grasses

Marsh Location	Marsh Grasses Present	References
St. Louis Bay Estuary, Miss.	Dominant species Juncus Roemerianus Spartina alterniflora Spartina patens Distichlis spicata Minor species Juncus effusus Panicum virgatum Panicum amarulum Zizaniopsis miliaceae Phragmites communis Scirpus americanus Scirpus robustus Scirpus californicus Scirpus Olneyi Scirpus validus Scirpus sp. Fimbristylis castanea Fimbristylis caroliniana Eleocharis cellulosa Eleocharis intermedia Cyperus odoratus Aster tenuifolius Aster subulatus Aster sp. Solidago sempervirens Ambrosia artemisiifolia Iva frutescens Sagittaria falcata Crinum americanum Lilaeopsis chinensis Amelopsis sp. Iris virginica Ipoema sagittaria Lythruna lineare	Gabriel and de la Cruz, 1974
Louisiana Coastal Marshes	Dominant species Spartina patens Spartina alterniflora Juncus Roemerianus Distichlis spicata Minor species Aenida alabamensis	Chabreck, 1972

(Continued)

(Sheet 1 of 3)

Marsh Location	Marsh Grasses Present	References
	Aster sp.	
	Avicennia nitida	
	Baccharis halimifolia	
	Bacopa Monnieri	
	Bacopa rotundifolia	
	Batis maritima	
	Borrichia frutescens	
	Cyperus odoratus	
	Echinochloa Walteri	
	Eleocharis parvula	
	Eleocharis sp.	
	Fimbrystylis castanea	
	Gerardia maritima	
	Ipomoea sagittata	
	Iva frutescens	
	Leptochloa filiformis	
	Lycium carolinianum	
	Lythrum lineare	
	Panicum virgatum	
	Paspulum vaginatum	
	Phragmites communis	
	Pluchea camphorata	
	Salicornia Bigelovii	
	Salicornia virginica	
	Scirpus Olneyi	
	Scirpus robustus	
	Scirpus validus	
	Spartina cynosuroides	
	Spartina spartineae	
	Suaeda linearis	
	Vallisneria americana	
	Vigna repens	
Gulf and Atlantic Coast, Northern Florida	Dominant species Spartina alterniflora Juncus Roemerianus	Kurz and Wagner, 1957
	Minor species Achyranthes philoxeroides Andropogon glomeratus Andropogon virginicus Aster tenuifolius Borrichia frutescens Chactochloa geniculata Chloris neglecta	

(Continued)

Marsh Location	Marsh Grasses Present	References
	Cymodocca manatorum	
	Cyperus erythrorhizos	
	Fimbristylis castanea	
	Halodule Wrightii	
	Halophila Engelmannii	
	Iva frutescens	
	Limonium carolinianum	
	Lyorria palustris	
	Muhlenbergia capillaris	
	Panicum virgatum	
	Paspalum vaginatum	
	Salicornia perennis	
	Solidago mexicana	
	Spartina bakeri	
	Spartina patens	
	Spartina spartinae	
	Thalassia testudinum	
	Uniola laxa	
Atlantic Coast, N. C.	Major salt marsh species Spartina alterniflora Spartina europaea Juncus Roemerianus Spartina perennis Limonium carolinianium Aster tenuifolius Distichlis spicata Borrichia frutescens Fimbrystylis castanea Spartina patens	Adams, 1963
Atlantic Coast, General	Dominant species Spartina alterniflora Spartina patens	Valiela and Vince, 1976

Table A3

Composition of Salt Marsh Compartment I-C, Soil and Epiphytic Algae

Type of Alga	Location	Species	References
Epiphytes	Barataria Bay, La.	Achnanthes Amphiprora Amphora Bostrychia Camphylodiscus Cladophora Cocconeis Cylindrotheca Cymbella Derrticula Diploneis Ectocarpus Enteromorpha Erythrotrichia Grammatophora Lyngbya Melosira Navicula Nitzschia Oscillatoria Pleurosigma Polysiphonia Rhizoclonium Rhopalodia Spirulina Surirella	Stowe et al., 1971 Day et al., 1973
Benthic and soil algae	Barataria Bay, La.	Achnanthes Amphiprora Amphora Anaulua Caloneis Cocconeis Cosmiodiscus Diploneis Eunotogramma Gyrosigma Mastogloia Melosira Navicula Nitzschia Plagiogramma Pleurosigma Rhaphoneis	Stowe et al., 1971 .Day et al., 1973

(Continued)

(Sheet 1 of 3)

Type of Alga	Location	Species	References
		Stauroneis Surirella Trachysphenia	
Epiphytic algae	Delaware salt marsh	Enteromorpha sp. Various filamentous and foliaceous green algae	Gallagher and Daiber, 1974
Soil algae	Banks and bare mud pans Delaware salt marsh (summer)	Blue-green algae Diatoms	Gallagher and Daiber, 1974
Soil algae	Sapelo Island, Ga.	Blue-green algae, dinoflagellates, green flagellates, pennate diatoms	Pomeroy, 1959
Soil algae	Under salt marsh grasses Great Sippewisset Salt Marsh, Md.	Calothrix contarenii Lyngbya aestuarii	Van Raalte et al., 1974
Soil algae	Great Sippewisset Salt Marsh, Md.	Amphiprora Cladophora Diploneis Lyngbya Microcoleus Nitzochia Oscillatoria sp. Vancheris sp.	Estrada et al., 1974
Soil algae	Great Sippewisset Salt Marsh, Md.	Achnanthes spp. Amphora spp. Biddulphia spp. Caloneis spp. Cocconeis spp. Cymbella spp. Diploneis spp. Fragilaria spp. Grammatophora spp. Gyrosigma spp.	Van Raalte et al., 1976b

(Continued)

Table A3 (Concluded)

Type of Alga	Location	Species	References
		Melosira spp.	
		Navicula salinarum	
		Nauiculum spp.	
		Nitzschia spp.	
		Opephora spp.	
		Pinnularia spp.	
		Pleurosigma spp.	
		Rhaphoneis spp.	
		Stauroneis spp.	
		Surriella spp.	
		Tropidoneis spp.	

Table A4

Composition of Salt Marsh Compartment I-D, Salt Marsh Herbivores

Name	Marsh Location	Food	Reference
Orchemliumum sp. (grasshopper)	Sapelo Island, Ga.	Marsh grasses, aboveground portion	Smalley, 1958
Ondatra zibethicus (muskrat)	East Coast marshes	Marsh grasses, roots	Teal and Teal, 1969
Myocastor coypus (nutria)	Gulf Coast marshes	Marsh grasses, roots	Chabreck, 1972
Littorina irrorata (marsh periwinkle)	Sapelo Island, Ga.	Algal filaments, epiphytic algae, epipelic algae, detritus	Smalley, 1958
Neritina reclivata (smooth periwinkle)	Louisiana marshes	Epipelic algae, epiphytic algae	Day et al., 1973
Melampus bidentaturus (small snail)	Louisiana marshes	Epipelic algae, epiphytic algae	Day et al., 1973
Modiolus demissus (ribbed mussel)	Sapelo Island, Ga.	Phytoplankton epiphytic and epibenthic algae loosened and carried around by tides	Kuenzler, 1961
Uca Pugnal (fiddler crab)	Sapelo Island, Ga.	Epipelic algae	Teal, 1958
Sesarma sp.	Gulf Coast	Algae	Personal Communication, April, 1975, Ivan Valiela, Associate Professor, Boston University Marine Program, Marine Biological Laboratory, Woods Hole, Mass.
Green crabs	East Coast marshes	Algae	

Table A5

Composition of Salt Marsh Compartment I-F, Salt Marsh Detritivores

Name	Marsh Location	Food	Reference
Littorina irrorata (marsh periwinkle)	Gulf Coast marshes Sapelo Island, Ga.	Detritus, Algal filaments Epiphytic and Epibenthic algae	de la Cruz, 1973 Smalley, 1958 Day et al., 1973
Melampus bidentaturus (small snail)	Gulf Coast marshes	Detritus, Epipelic and Epiphytic algae	de la Cruz, 1973 Day et al., 1973
Uca pugnax (fiddler crab)	Sapelo Island, Ga.	Detritus, Epipelic algae	Teal, 1958, de la Cruz, 1973
Corophium sp. Ampilesca sp. (amphipods)	Louisiana marshes	Detritus	Day et al., 1973

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Table A6

Composition of Salt Marsh Compartment I-G, Salt Marsh Carnivores

Organism	Food Source	Reference
Procyon lotor (raccoon)	Molluscs, crabs	Day et al., 1973
Circus cyaneus (marsh hawk)	Mice, birds, other small animals	Teal and Teal, 1969
Mustela vison (mink)	Mice, other small animals	
Various shorebirds	Marsh insects, annelids, amphipods	Teal and Teal, 1969 Day et al., 1973
Various spiders	Marsh insects	Personal Communication, Dec. 1974, William Pfeiffer, Biologist, Georgia Institute of Marine Science, Sapelo Island, Ga.
Rallus longirostris (clapper rails)	Snails, crabs, insects, spiders	Oney, 1954 Bateman, 1965

Table A7

Composition of Estuary Compartment II-B, Estuarine Sediment

		Occurrence in Sediments		
Constituent, % of total	Gulf Coast (Alabama)*	NE Atlantic Coast (Connecticut)*	NW Pacific Coast (Washington)**	Australia (Victoria)†
Sand (<50 micrometers)	14.8	3.5	N/A	N/A
Silt (<2 micrometers)	52.7	58.2	N/A	N/A
Clay (2-50 micrometers)	32.5	38.3	N/A	N/A
Organic matter (total organic carbon)	2.03	2.69	0.13-4.70	0.1-2.3
Total nitrogen (µg/g)	1900	2680	N/A	N/A
Total sulfides (µg/g)	903	2680	N/A	N/A
Total metals (µg/g)				
arsenic	4.08	6.90	3-15 ppm	N/A
cadmium	3.62	17.60	N/A	0.04-0.06
chromium	N/A††	N/A	40-200 ppm	N/A
copper	N/A	N/A	N/A	0.29-87 ppm
lead	N/A	N/A	N/A	1.8-183 ppm
mercury	N/A	N/A	0.01-0.1 ppm	N/A
nickel	156	203	N/A	N/A
zinc	243	1067	N/A	2.9-278 ppm

* Data from Brannon et al., 1976
** Data from Crecelius et al., 1975
† Data from Talbot et al., 1976
†† N/A = Data not available

Table A8

Composition of Estuary Compartment II-C, Periphyton and Rooted Macrophytes

Type of Plant	Name	Occurrence	Reference
Periphytic algae			
Chlorophyceae	Ulvella sp. Ulothrix sp. Cladophora sp. Rhizoclonium sp.	Benthos, tidal mud flats, shallow tide pools	Kapraun personal communication as cited in Day, et al., 1973
Oscillatoriaceae	Lyngbya sp.	Minor component of benthic algal mats	
	Oscillatoria sp.	O. princeps often a dominant in benthic algal mats	
	Spirulina sp.	Minor component in benthic algal mats	
Chroorocaceae	Anacystis sp. Chroorocorcus sp. Merismopedia sp.	Present in benthic algal mats	
Bacilliarophyceae	Amphiprora sp. Amphora sp. Caloneis sp. Cylindrotheca sp. Denticula sp. Diploneis sp. Gyrosigma sp. Mastogloria sp. Navicula sp. Nitzschia sp. Opephora sp. Paralia sp. Pleurosigma sp.	Benthic diatoms	
Macrophytic algae	Bostrychia rivularis Cladophora repens Cladophora gracilis Ectocarpus sp. Enteromorpha flexiosa Gracilaria foliifera Ulva lactuca		
Rooted macrophytes	Zostera marina	Bering Straits to Baja, Calif.; Greenland to Cape Fear, N. C.	Thayer et al., 1975
	Thalassia testudinum	Florida coast	Zieman, 1975

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Table A9

Composition of Estuary Compartment II-E, Phytoplankton

Algae	Estuary	Reference
Actinoptychus	Barataria Bay, La.	Day et al., 1973
Biddulphia		
Ceratium		
Chaetoceros		
Coscinodiscus		
Cylindrothera		
Dinophysis		
Ditylum		
Gonyanlax		
Merismopedia		
Nitzschia		
Peridinium		
Prorocentrum		
Rhizosolenia		
Exuviella apora	Long Island Sound	Riley, 1967
Paralia sulcata		
Peridinium trochoideum		

Composition of Salt Marsh Compartment I-E and Estuary Compartment II-F (Detritus-Decomposers)

Detritus Source	Location and Type of Marsh	Decomposition Rate (%/yr)	Reference
Marsh grasses			
Spartina spp.	Barataria Bay, La.		
	High marsh	80*	Kirby, 1971
	Streamside	89*	
	Tidal creek	96*	
	Bay St. Louis, Miss.		
	High marsh	52*	de la Cruz, 1973
	Sapelo Island, Ga.		
	High marsh	50*	de la Cruz, 1965
	Streamside marsh	60*	
	Levee, marsh	65*	
	Marsh creek	88**	Burkholder and Bornside, 1957
Juncus Roemerianus	Bay St. Louis, Miss.	40*	de la Cruz and Gabriel, 1973
	Sapelo Island, Ga.	35*	de la Cruz, 1965
	Bodie Island. N. C.	47*	Waits, 1967
	North of Cape Lookout, N. C.	46+	Williams and Murdock, 1972
Distichlis spicata	Bay St. Louis, Miss.	38*	Gabriel and de la Cruz, 1974

(Continued)

* Employed nylon bags of 1- to 5-mm mesh.
** Employed lath crates, 10-mm mesh.
+ Measured disappearance rate without a container.

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Table A10(a) (Concluded)

Detritus Source	Location and Type of Marsh	Decomposition Rate (%/yr)	Reference
	Sapelo Island, Ga.	53*	de la Cruz, 1965
Salicornia sp.	Sapelo Island, Ga.	94*	de la Cruz, 1965
Scirpus americanus	Bay St. Louis Miss.	60*	de la Cruz, 1973
Kelps			
Laminaria sp.	Atlantic Coast of Canada	N/A++	Mann, 1972
Macrocystis sp.	California Coast	N/A	
Sea Grasses			
Thalassia sp.	Southern U. S. Gulf Coast	N/A	Mann, 1972
Zostera sp.	Atlantic Coast, U. S.	N/A	
Rooted Algae			
Fucus sp.	Nova Scotia	N/A	Mann, 1972
Ascophyllum sp.	Nova Scotia	N/A	
Mangrove Leaves			
Red Mangrove	Puerto Rico	62	Mann, 1972
White Mangrove		N/A	Heald, 1969

++ Not available.

Table A10(b)

Composition of Salt Marsh Compartment I-E and Estuary Compartment II-F

(Microbial Decomposer Compartment)

	Constituent	Substrate/Location	References
1.	Bacteria		
	a. Organisms able to use marsh grass extracts	Spartina/Georgia	Burkholder and Bornside, 1957
	Aerobacter sp. _Flavobacterium_ sp. _Pseudomonas_ sp. _Serratia_ sp.		
	b. Dominant bacteria in soil	Submerged sediments/ Louisiana marshes	Hood, 1970
	(1) Aerobes		
	Bacillus sp. _Pseudomonas_ sp.		
	(2) Anaerobes		
	Clostridium sp. _Micrococcus_ sp. _Sarcina_ sp.		
	c. Predominant bacteria in estuarine water	Louisiana Coastal waters	Hood, 1970
	Vibrio sp. _Pseudomonas_ sp. _Achromobacter_ sp.		
2.	Yeasts associated with marsh grasses and soils _Pichia_ sp. _Kluyveromyces_ sp.	Viable green marsh grass tissue, brown stem material undergoing dieback/Louisiana marshes	Ahearn et al., 1970 Meyers, 1974
3.	Fungi		
	Fungi associated with "die back" of _Spartina_ sp. _Cephalosporium acremonium_	_Spartina_ plant roots, stems, rhizomes/English marshes	Sivanesan and Manners, 1970
4.	Nutritional types of bacteria		Hood and Colmer, 1971
	a. Proteolytic species (50-60 percent)		
	b. Lipolytic and Alginolytic species (40 percent)		
	c. Cellulolytic species (low concentration)		
	d. Sulfate reducers (predominant physiological form in the anaerobic zone)		
5.	Bacteria dominant on marsh soil surface _Pseudomonas_ sp. _Vibrio_ sp. _Bacillus_ sp.	Marsh soil plus bottom 1/2 in. of _Spartina_ stalk/Louisiana marshes	Hood and Colmer, 1971

(Continued)

Table A10(b) (Concluded)

Constituent	Substrate/Location	References
6. Marine bacteria associated with marsh plants	Attached to _Spartina_ plant/ Louisiana Coastal marshes	Hood and Colmer, 1971
Bacillus sp. _Cladosporium_ _herbarum_ _Fusarium_ _solani_ _Pencillium_ _digitatum_ _Pencillium_ _freguentans_ _Pencillium_ _variabile_ _Trichodermum_ _koningi_		
7. Fungi attacking _Spartina_ by mycota during development and decomposition		
Sphaerulina _pedicellata_	Growth stage of _Spartina_ _alterniflora_/Rhode Island	Gessner et al., 1972
Leptosphaeria sp. _Haligenia_ sp. _Pleospora_ sp. _Lulworthia_ sp.	Browing stage of _Spartina_ _alterniflora_/Rhode Island	
8. Bacteria dominant on marsh soil surface	Marsh soil plus bottom 1/2 in. of _Spartina_ stalk/Louisiana marshes	
Pseudomonas sp. _Vibrio_ sp. _Bacillus_ sp.		
9. Marine bacteria associated with marsh plants	Attached to _Spartina_ plant/ Louisiana Coastal marshes	Hood and Colmer, 1971
Bacillus sp.		

Table A11

Composition of Estuary Compartment II-G, Herbivores

Name	Estuary Location	Food	References
Penaeus dunarum (pink shrimp)	Louisiana	Benthic diatoms, filamentous green algae, filamentous blue-green algae	Odum, 1971
Penaeus aztecus (brown shrimp)	Louisiana	"	Jacob and Loesch, 1971
Penaeus setiferus (white shrimp)	Louisiana	"	Jacob and Loesch, 1971
Palaemonetes vulgaris (grass shrimp)		"	Day et al., 1973
Palaemonetes pugio (grass shrimp)		"	Day et al., 1973
Trachypeneus similis (penaeid shrimp)		"	Day et al., 1973
Xiphopeneus kroyeri (seabob)		"	Day et al., 1973
Alpheus heterochaelis (snapping shrimp)		"	Day et al., 1973
Adenia fenica (diamond killifish)	Florida	Benthic diatoms	Forman, 1968 Odum, 1971
Mugil cephalus (stripped mullet)	Louisiana Florida	Vascular plants, blue-green algae, diatoms, filamentous algae, green algae	Darnell, 1961 Odum, 1971 Day et al., 1973
Cyprinodon variegatus (sheepshead minnow)	Louisiana	Algae, plant fibers	Hildebrand and Schroeder, 1928 Forman, 1968 Odum, 1971
Fundulus grandis (Gulf killifish)	Florida	Filamentous algae	Odum, 1971
Fundulus confluentus (marsh killifish)	Florida	Algae filaments	Odum, 1971

(Continued)

Table A11 (Concluded)

Name	Estuary Location	Food	References
Poecilia latipinna (sailfin molly)	Florida	Algae, diatoms	Odum, 1971
Acartia tonsa (copepod)	Gulf Coast, Atlantic Coast	Phytoplankton	Day et al., 1973 Riley, 1967
Miscellaneous species of copepods			Darnell, 1961

Table A12

Composition of Estuary Compartment II-H, Detritivores

Name	Estuary Location	Food*	References
Mugil cephalus (stripped mullet)	Mississippi Sound, Louisiana	Detritus, vascular plants, diatoms filamentous algae, blue-green algae, green algae	Darnell, 1961, 1976 Day et al., 1973 de la Cruz, 1973
Brevoortia patronus (Gulf menhaden)	Louisiana	Detritus, zoo-plankton, phyto-plankton	June and Carlson, 1971 Odum, 1971 de la Cruz, 1973
Fundulus heteroclitus (Atlantic killifish)	Louisiana Florida	Detritus	Odum, 1971 de la Cruz, 1973
Adenia xenica (diamond killifish)	Louisiana Florida	Detritus	Odum, 1971
Fundulus confluentus (marsh killifish)	Louisiana Florida	Detritus, algal filaments	Odum, 1971 de la Cruz, 1973
Cyprinodon variegatus (sheepshead minnow)	Louisiana Florida	Detritus, algae, plant fibers	Hildebrand and Schroeder, 1928 Forman, 1968 Odum, 1971 de la Cruz, 1973
Anchoa mitchelli (bay anchovy)	Florida	Detritus	Odum, 1971
Gambusia affinis (mosquitofish)	Gulf coast	Detritus	de la Cruz, 1973
Mollienisa (poecillia) latipinna (sailfin molly)	Gulf Coast	Detritus, algae	Odum, 1971 de la Cruz, 1973
Rithropanopeus harrisii (crab)	Florida	Detritus	Odum, 1971
Sesarma sp.	Gulf Coast	Detritus	de la Cruz, 1973
Penaeus pugio (grass shrimp)	Gulf Coast	Detritus	de la Cruz, 1973
Alpheus heterochaelis	Gulf Coast	Detritus	de la Cruz, 1973

* Since detritus is rarely the sole food of any detritivores, other food are also given.

Table A13

Composition of Estuary Compartment II-I, Carnivores

Name	Estuary Location	Food	References
Brevoortia patronus (Gulf menhaden)	Louisiana	Zooplankton, phytoplankton, detritus	Darnell, 1958
Brevoortia tyrannus (Atlantic menhaden)	Atlantic Coast	Zooplankton and phytoplankton (juvenile fish)	June and Carlson, 1971
		Zooplankton and detritus (adult fish)	Jeffries, 1975
Leiostomus zanthurus (spot)	Gulf Coast	Vascular plants, copepods, ostracods (Texas)	Parker, 1971
		Pelecypods, detritus, copepods, (Louisiana)	Parker, 1971
		Crustaceans, annelids, small molluscs, fish, detritus	Pearson, 1928
		Copepods, nematodes diatoms, formaniferans	
		Zooplankton, insect larvae, fish	Day et al., 1973
Adenix xenica (diamond killifish)	Florida	Small amphipods, copepods, small insects, vascular plant detritus, benthic diatoms	Odum, 1971
		Detritus, diatoms, small crustaceans, insects	Forman, 1968
Fundulus grandis (Gulf killifish)	Gulf Coast	Amphipods, isopods, xanthid crabs, chironomid larvae, terrestrial insects, small gastropods, filamentous algae, polychaetes, insects, small fish, crab megalops, nematodes	Forman, 1968 Odum, 1971 Day et al., 1973
Fundulus confluentus (marsh killifish)	Florida	Small fish, amphipods isopods, adult and larval insects, copepods, mysids, ostraiods, algal filaments	Odum, 1971
		Copepods, annelids, fish (Florida)	Townsend, 1956
		Ostracods, harpacticold copepods, detritus, vascular plants	Darnell, 1958
		Planktonic and dermersal crustaceans, annelids	Dawson, 1958
		Amphipods calanoid copepods, detritus	Thomas et al., 1971
Cynoscion arenarius (sand seatrout)	Louisiana	Fish, macrobenthic species, zooplankton, detritus, amphipods, fish, microbenthic spp.	Darnell, 1958 Day et al., 1973
Menidia beryllina (tidewater silversides)	Louisiana	Amphipods, isopods, chironomid larvae detritus, zooplankton, vascular plants	Darnell, 1958
	Florida	Copepods, Mysids, amphipods, terrestrial insects, chironomid larvae	Odum, 1971
Callinectes sapidus (blue crab)	Gulf Coast	Zooplankton	Tagatz, 1968 Odum, 1971 Day et al., 1973

Table A14

Cycling of Carbon in Marsh-Estuarine Ecosystems as Described by the General Compartmental Model

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
I-A Marsh soil	Organic carbon added by death of plants or accumulation from deposited sediment	Accumulation rates in marsh soil: Initial level--12.2 g C/m^2 Bare soil accumulation--80.3 gC/m^2 Soil with _Spartina_--87.0 $gC:m^2:yr$ Fertilized soil with _Spartina_--96.8 $gC:m^2:yr$ Turnover time for carbon in soil-- 3.7-4.5 yr	Cammen, 1975

	Organic matter in marsh soil from _Spartina_ marsh		Organic Matter, %		Broome et al., 1973
		Marsh Site (All North Carolina)	Short Grass Marsh	Tall Grass Marsh	
		Oregon Inlet	0.1	0.1	
		Ocracoke	0.3	0.7	
		Hatteras Village	0.3	5.1	
		North River	10.8	1.6	
		Beaufort	6.0	5.0	
		Swansboro	0.5	1.1	
		Oak Island	6.5	9.3	

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
Arrow No. 1 (I-A, I-B)	Inorganic carbon	Insignificant	Teal and Kanwisher, 1961
Arrow No. 1 (I-B, I-A)	Inorganic carbon	Release to soil water by marsh grass roots is sufficient to add 20-30 mℓCO/ℓ of water to marsh creek waters by the time tidal waters have left marsh surface via percolation of water through soil	Teal and Kanwisher, 1961
	Organic carbon excreted by marsh grass roots into soil interstitial waters	Not available for salt marsh plants	
		Available for freshwater emergent macrophytes	Wetzel and Rich, 1973
Arrow No. 2 (I-A, I-C)	Inorganic carbon in interstitial water	Described for benthic diatoms in sand, but specific uptake rates not available	Baird and Wetzel, 1972
	Dissolved organic carbon (DOC)	Possible source of DOC for heterotropic uptake by soil algae. Has not been studied for specific marsh soil and epiphytic algae, but has been documented for planktonic species	Hellebust, 1967
Arrow No. 2 (I-C, I-A)	Inorganic carbon	Specific rates of CO_2 release by respiration to soil water have not been measured	
	DOC	Release of DOC to interstitial water of marsh soil has not been studied. However, release of DOC to water is inferred on the basis of the following:	
		1.0 soil algae actively conduct photosynthesis at depths of up to a few mm in marsh soils	
		2.0 algae release DOC during photosynthesis. This enters surrounding millieu	Hellebust, 1967
		3.0 many species of algae produce extracellular slimes which are elaborated on the cell surface and which are then solubilized--a mechanism which prevents build up of epiphytes and other microbes on cell surfaces	Smith, 1950
Arrow No. 2 (I-C, I-A)	Particulate organic carbon (POC)	Death of soil algae within soil matrix is a source of POC to marsh soil, but rates and quantities are _unknown_	

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage		Reference
I-B Marsh grasses	Organic carbon _Spartina alterniflora_	Production data in g dry weight:m^2:yr. Carbon content is approximately one-half of this:		
		445	Delaware	Morgan, 1961
		1207	Maryland	Johnson, 1970
		329-1296	North Carolina	Stroud and Cooper, 1969
		1000	North Carolina	Williams and Murdock, 1966
		650	North Carolina	Williams and Murdock, 1969
		2883	Georgia	Odum and Fanning, 1973
		2000	Georgia	Schelske and Odum, 1961
		985	Georgia	Smalley, 1959
		1089-1964	Mississippi	Gabriel and de la Cruz, 1974
		1150	Louisiana	Kirby, 1971

(Continued)

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
I-B Marsh grasses (Continued)	Organic carbon Spartina alterniflora (Continued)	Percent carbon content of Spartina alterniflora 40.77 Georgia 38.3 Long Island, New York 38.8 North Carolina	Burkholder, 1956 Udell et al., 1969 Williams, 1972
	Organic carbon Spartina cynosuroides	Production in g dry weight:m^2:yr 1028 Georgia 2190 Mississippi	Odum and Fanning, 1973 Gabriel and de la Cruz, 1974
		Percent carbon content of Spartina cynosuroides, 32.10	Gabriel and de la Cruz, 1974
	Organic carbon Spartina patens	Production in g dry weight:m^2:yr 993 New York 1296 North Carolina 1922 Mississippi	Harper, 1918 Waits, 1967 Gabriel and de la Cruz, 1974
		Percent carbon contents of Spartina patens 5.26 29.36	Chabreck, 1972
	Organic carbon Juncus Roemerianus	Production in g dry weight:m^2:yr 560 North Carolina 796 North Carolina 1360 North Carolina 849 Florida 1697 Mississippi	Foster, 1968 Stroud and Cooper, 1969 Waits, 1967 Heald, 1969 Gabriel and de la Cruz, 1974
		Percent carbon content of Juncus Roemerianus 36.6 26.45 44.3	de la Cruz and Gabriel, 1973 Chabreck, 1972 Gallagher, 1974
	Organic carbon Distichlis spicata	Production in g dry weight:m^2:yr 1484 Mississippi	Gabriel and de la Cruz, 1974
		Percent carbon content of Distichlis spicata, 23.64	Chabreck, 1972
	Organic carbon Scirpus robustus	Production in g dry weight:m^2:yr 1056 Mississippi	de la Cruz, 1974
		Percent carbon content of Scirpus robustus, 23.15	Chabreck, 1972
I-C Soil algae	Organic carbon	Production in g C:m^2:yr 200 Georgia--marsh soil 79-99 Delaware--marsh soil 244 Louisiana	Pomeroy, 1959 Gallagher and Daiber, 1974 Brkich as cited in Day et al., 1973
I-C Epiphytes	Organic carbon	Production in g C:m^2:yr 103.9 on Spartina, Louisiana 10 average over Barataria Bay marshes, Louisiana	Stowe, 1971 Day et al., 1973
Arrow No. 3 (I-B, I-E)	Organic carbon	90-95% of annual production	Teal, 1962
Arrow No. 4 (I-B, I-D)	Organic carbon	5-10% of annual production	Teal, 1962
Arrow No. 5 (I-C, I-D)	POC	No valid estimates are available from current literature or other sources	
Arrow No. 6 (I-C, I-E)	POC	No valid estimates are available from current literature or other sources	
I-D Marsh herbivores	Organic carbon	No data are available on total marsh herbivore production	
Arrow No. 7 (I-D, I-G)	Organic carbon	No valid estimates are available from current literature or other sources	

(Continued)

(Sheet 2 of 6)

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
Arrow No. 8 (I-D, I-E)	Organic carbon	No valid estimates are available from current literature or other sources	
Arrow No. 9 (I-E, I-F)	POC	Approximately 500 gC:m^2:yr are consumed by detritivores and by microbial decomposition processes on the marsh (Arrow No. 12 (I-E1, I-E2))	Day et al., 1973
Arrow No. 9 (I-F, I-E)	Organic carbon	No valid estimates are available from current literature or other sources	
Arrow No. 10 (I-F, I-G)	Organic carbon	No valid estimates are available from current literature or other sources	
Arrow No. 11 (I-G, I-E)	Organic carbon	No valid estimates are available from current literature or other sources	

Arrow No. 12 (I-E1, I-E2) — Organic carbon from _Spartina_ spp. leaves

Decomposition rates of various detritus substrates (%/year)

		Georgia (Sapelo Island)	
	50	High marsh	de la Cruz, 1965
	65	Levee marsh	de la Cruz, 1965
	60	Streamside marsh	de la Cruz, 1965
	88	Marsh creek	Burkholder and Bornside, 1957
		Mississippi (Bay St. Louis)	
	52	High marsh	de la Cruz, 1973

Decomposition rates of various detritus substrates (%/year)

		Louisiana (Barataria Bay)	
	80	High marsh	Kirby, 1971
	89	Streamside marsh	
	96	Marsh creek	
Juncus roemerianus leaves	47	North Carolina	Waits, 1967
	35	Georgia (Sapelo Island)	de la Cruz, 1965
	36	Florida (Everglades)	Heald, 1969
	40	Mississippi (Bay St. Louis)	de la Cruz and Gabriel, 1973
Distichlis spicata leaves	94	Georgia (Sapelo Island)	de la Cruz, 1965
	38	Mississippi (Bay St. Louis)	**Gabriel and de la Cruz, 1974**
Salicornia sp. leaves	94	Georgia (Sapelo Island)	de la Cruz, 1965
Red mangrove leaves	60	Florida (Everglades)	Heald, 1969
White mangrove leaves	38	Florida (Everglades)	Heald, 1969

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
Arrow No. 12 (I-E2, I-E1)		_No valid estimates are available from current literature or other sources_	
Arrow No. 13 (I-E, I-A)	POC	_No valid estimate has been made since an estimated 45% is exported to the estuary/ year; whatever of the remaining 55% which is not consumed by detritivores must become part of marsh soil or be decomposed to CO_2_	Teal, 1962
Arrow No. 13 (I-A, I-E)	Organic carbon (as live cells)	Inconsequential--serves as a reservoir of inoculum for new detrital materials	
I-E Detrites microbial decomposers	Organic carbon	Actual masses of detritus have not been measured	
I-F Detritivores	Organic carbon	Specific estimates of total detritivore biomass and carbon contents not available from current literature or other sources	
I-G Carnivores	Organic carbon	Specific estimates total carnivore biomass and carbon contents not available from current literature or other sources	
Arrow No. 14 (I-B, I-C)	None	No carbon transferred	
Arrow No. 15 (II-B, II-C)	Inorganic carbon	Little or no inorganic carbon is taken up this way	
Arrow No. 15 (II-C, II-B)	Inorganic carbon	No information available on root respiration rates and carbon dioxide release by roots	

(Continued)

Table A14 (Continued)

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
Arrow No. 15 (II-C, II-B) (Continued)	Organic carbon	Release of organic carbon from roots to sediments in either dissolved or particulate form has not been documented	
II-C Periphytic algae	Organic carbon	Production in g dry weight:m^2:yr	
	Microbenthic algae	400 Georgia (Sapelo Island)	Pomeroy, 1959
	Benthic algae	370 Louisiana (Barataria Bay)	Day et al., 1973
	Ulva lactuca	785 New York	Udell et al., 1969
II-C Rooted macrophytes	Organic carbon	Production in g dry weight:m^2:yr	
	Thalassia testudinium	5660 Puerto Rico	Burkholder et al., 1959
	Zostera marina	2464 New York	Udell et al., 1969
	Zostera marina	66 Rhode Island	Nixon and Oviatt, 1973
II-D Dissolved mineral pool	Inorganic carbon	Average concentration	Teal, 1967
		1.61 mg C/ℓ Woods Hole, Mass.	
	Amino acids	10^{-5} moles/ℓ--sea water, California coast	Stephans, 1967
		2.5×10^{-5} moles/ℓ--interstitial water, California coast	
		$10^{-5} - 10^{-4}$ miles/ℓ inshore water, California coast	
	DOC--general	1.8-2.25 mg C/ℓ--sea water	Field, 1972
	Dissolved organic matter	Material under m.w. 500	
		0.67 mg C/ℓ Tokyo Bay	Ogura, 1975
		Total dissolved organic matter	
		2.89 mg C/ℓ Tokyo Bay	Ogura, 1975
		1.41 mg C/ℓ Sagami Bay	Ogura, 1975
		1.10 mg C/ℓ W. North Pacific	Ogura, 1972
Arrow No. 17 (II-B, II-D)	Inorganic carbon Methane DOC	General evolution and release rates unknown	
Arrow No. 17 (II-D, II-B)	Inorganic carbon DOC	General diffusion and sorption rates unknown	
Arrow No. 18 (II-D, II-E)	Inorganic carbon	0.2 mg C:ℓ:hr	Teal, 1967
	Organic carbon	No data for phytoplankton as a whole	
Arrow No. 18 (II-E, II-D)	Inorganic carbon		
	Organic carbon	No estimates available for natural populations. Values for pure cultures vary	Hellebust, 1967
II-E Phytoplankton	Organic carbon	Production in g dry weight:m^2:yr	
		Washington	
		380 Upwelling north of river	Anderson, 1964
		220 River mouth	
		152 Ocean beyond river	Anderson, 1964
		150 River plume	
		New York	
		987 Hempstead Bay, Long Island	Udell et al., 1969
		512 Long Island Sound	Riley, 1956
		400 Shallow coastal water off New York	Ryther and Yentsch, 1958
		300 Continental Shelf area	Ryther and Yentsch, 1958
		250 Continental Slope	Ryther and Yentsch, 1958
		1368 Coastal water, Georgia	Thomas, 1966
		418 Louisiana (Barataria Bay)	Day et al., 1973
II-F Detritus--microbial decomposers	POC	35-42 g/m^3--Louisiana (Barataria Bay)	Cruz-Orozco, 1970
Arrow No. 19 (II-E, II-G)	Organic carbon	75% of net annual production--Louisiana (Barataria Bay)	Day et al., 1973
Arrow No. 20 (II-C, II-G)	Organic carbon	No data	
Arrow No. 21 (II-C, II-F)	Organic carbon	No data	

(Continued)

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
Arrow No. 22 (II-E, II-F)	Organic carbon	25% of net annual production (extrapolation) Louisiana (Barataria Bay)	Day et al., 1973
II-G Estuarine herbivores	Organic carbon	2.5 g:m^2:yr zooplankton 1.0 g:m^2:yr others Louisiana (Barataria Bay)	Day et al., 1973
II-H Detritivores	Organic carbon	3.48 g C:m^2:yr	Day et al., 1973
Arrow No. 23 (II-G, II-I)	Organic carbon	No data. Estimate of 21 g C:m^2:yr	Day et al., 1973
Arrow No. 24 (II-F, II-H)	Organic carbon	No data	
Arrow No. 24 (II-H, II-F)	Organic carbon	No data	
Arrow No. 25 (II-H, II-I)	Organic carbon	No data	
Arrow No. 26 (II-I, II-F)	Organic carbon	No data. Estimate of 9.53 g C:m^2:yr (top carnivore production) (Barataria Bay, La.)	Day et al., 1973
Arrow No. 27 (II-G, II-F)	Organic carbon	No data	
Arrow No. 28 (II-D, II-F)	DOC	Little direct transfer except for dissolved organic matter sorbed onto detritus and de novo synthesis of detritus from dissolved materials. No data	Baylor and Sutcliff, 1963
Arrow No. 28 (II-F, II-D)	DOC	Up to 82% of dry weight of Zostera marina can be leached out. No data for others	Harrison and Mann, 1975
Arrow No. 29 (II-H, II-D)	DOC	Urea—no data for populations	
	Inorganic carbon	Respiration—no data for populations	
Arrow No. 29 (II-D, II-H)	DOC	None	
Arrow No. 30 (II-D, II-I)	DOC	None	
Arrow No. 30 (II-I, II-D)	DOC	Urea—no data for populations	
	Inorganic carbon	Respiration—no data for populations	
II-I Estuarine carnivores	Organic carbon	21 g C:m^2:yr—Louisiana (Barataria Bay)	Day et al., 1973
Arrow No. 31 (II-D, II-G)	DOC	No data	
Arrow No. 31 (II-G, II-D)	DOC	Urea—no data for populations	
	Inorganic carbon	Respiration—no data for populations	
Arrow No. 33a (II-E, II-B)	Particulate organic matter	Primarily bones that contain carbonates plus undecomposable residues—no data	
33b (II-G, II-B)			
33c (II-I, II-B)			
33d (II-F, II-B) (II-B, II-F)			
33e (II-H, II-B)			
Arrow No. 34 (II-F1, II-F2)	Organic carbon	1 g detritus consumes 1 mg O_2/hr = 0.38 mg c:g detritus/hr Limnea feces consume 0.4-3.5 mg O_2: g:h = average 0.76 mg C:g feces:hr	Hargrave, 1972
Arrow No. 35A (flood)	Inorganic carbon	Probably have no net addition to marshes	
	Organic carbon	Most carbon brought onto marsh surface was originally generated there and is merely shuffled around by the tides	
Arrow No. 35B (ebb, flush, storm)	Inorganic carbon	20-30 ml CO_2/ℓ water added by respiration of marsh grass roots/tidal cycle	Teal and Kanwisher, 1962
	POC	3.4 tons:ha marsh:yr = 1.36 tons C:ha marsh: yr = 50% of marsh grass production	Odum and de la Cruz, 1967
Arrow No. 36 (III, II-A)	DOC	Highly variable and watershed specific	
	Dissolved Inorganic carbon		

(Continued)

Table A14 (Concluded)

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
Arrow No. 36 (II-A, III)		No valid estimates are available	
Arrow No. 37 (I, IV)	Inorganic carbon Spartina sp.	Respiration $\approx$ 3664 $g{:}m^2{:}yr$ = 1546 g $C{:}m^2{:}yr$	Teal, 1962
Arrow No. 37 (IV, I)	Inorganic carbon Spartina sp.	Spartina sp. grass production = 8452 $g{:}m^2{:}yr$ = 3384 g $C{:}m^2{:}yr$	Teal, 1962
Arrow No. 38 (II-A, IV)	Inorganic carbon	2×10^{-5} cm^2/sec diffusion air → water	Teal, 1967
Arrow No. 38 (IV, II-A)	Inorganic carbon	$<2 \times 10^{-5}$ cm^2/sec diffusion water → air	
Arrow No. 39A (flood)	Inorganic and organic carbon	No data	
Arrow No. 39B (ebb)	Inorganic and organic carbon	Net export to gulf = 42.4% of net production available to estuary or 30% of total net production of estuary = 356 g $C{:}m^2$ over total estuary area	Day et al., 1973

Table A15

Cycling of Nitrogen in Marsh-Estuarine Ecosystems as Described by the General Compartmental Model

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
I-A Marsh soil	Nitrogen	Percent nitrogen content of marsh soils (Louisiana coast): saline vegetative type 0.44, brackish type 0.72	Chabreck, 1972
Arrow No. 1 (I-A, I-B)	Inorganic nitrogen (nitrate, ammonium)	Nitrogen is limiting to plant growth; uptake rated in soil not detailed	Teal and Teal, 1969
Arrow No. 1 (I-B, I-A)	Organic nitrogen (dissolved and particulate) marsh grass roots	Evolution rates not detailed	
Arrow No. 2 (I-A, I-C)	Inorganic nitrogen (nitrate, ammonium)	Route for N supply to algae living within soil matrix -- no data	
Arrow No. 2 (I-C, I-A)	Dissolved organic nitrogen	Excretion and lysis of algae source of dissolved organic nitrogen. Amount unknown	
	Particulate organic nitrogen	Cell death provides organic nitrogen to soil	
I-B Marsh grasses		Percent nitrogen content	
	Spartina alterniflora leaves	0.8 live plants, North Carolina 0.7 dead plants 0.7 live plants, Georgia 0.7 dead plants 2.12 New York 1.40 0.54 2.23 1.31 1.18	Broome et al., 1973 Gallagher, 1975a Burkholder, 1956 Hall et al., 1970 Tachdjian, 1954 Udell et al., 1969 Stuckey, 1970 Williams, 1972
	Spartina cynosuroides leaves	0.45 Georgia 1.20 Florida	de la Cruz, 1973 Johnson, 1970
	Organic nitrogen	Percent nitrogen content:	
	Spartina patens leaves	1.04 _Louisiana_	Chabreck, 1972
	Juncus Roemerianus leaves	0.46 Mississippi Gulf Coast 0.85 1.45 Louisiana coastal marshes	Gabriel and de la Cruz, 1974 Stuckey, 1970 Chabreck, 1972
	Live	1.20 live, Georgia	Gallagher, 1975a
	Dead	0.8 dead, Georgia	Gallagher, 1975a
	Distichlis spicata	1.38 Louisiana	Chabreck, 1972
	Scirpus robustus	1.37 Louisiana	Chabreck, 1972
Arrow No. 3 (I-B, I-E)	Organic nitrogen	No data	
Arrow No. 4 (I-B, I-D)	Organic nitrogen	No data	
I-C Soil algae	Organic nitrogen	No data on nitrogen content of marsh algae	
Arrow No. 6 (I-C, I-E)	Particulate organic nitrogen	No data	
I-D Herbivores	Organic nitrogen	No data	
I-E Detritus-microbial decomposers	Organic nitrogen _Spartina alterniflora_	Percent nitrogen content of detritus: 2.12 2.23 1.18 1.31	Burkholder, 1956 Udell et al., 1969 Williams, 1972 Stuckey, 1970
	Spartina cynosuroides	0.45 1.20	de la Cruz, 1973 Johnson, 1970
	Juncus Roemerianus	0.78 0.95	de la Cruz, 1973 Williams, 1972
I-E Detritus-microbial decomposers	Organic nitrogen _Distichlis spicata_	Percent nitrogen content of detritus 0.46 0.85	de la Cruz, 1973 Stuckey, 1970
Arrow No. 7 (I-D, I-G)	Organic nitrogen	No data	
Arrow No. 8 (I-D, I-E)	Organic nitrogen	No data	
Arrow No. 9 (I-E, I-F)	Organic nitrogen	No data	
Arrow No. 9 (I-F, I-E)	Organic nitrogen	No data	
Arrow No. 10 (I-F, I-G)	Organic nitrogen	No data	
Arrow No. 11 (I-G, I-E)	Organic nitrogen	No data	
I-F Marsh detritivores	Organic nitrogen	No data for detritivore populations	
Arrow No. 12 (I-E1, I-E2)	Organic nitrogen	Computed from tabulated data:	
	Spartina alterniflora	16.98 g $N:m^2:yr$	de la Cruz, 1973
	Juncus Roemerianus	3.00 g $N:m^2:yr$	
	Distichlis spicata	4.01 g $N:m^2:yr$	
Arrow No. 13 (I-A, I-E)		No data	
Arrow No. 13 (I-E, I-A)		No data	
Arrow No. 14 (I-B, I-C)		No data	
Arrow No. 15 (II-B, II-C)	Inorganic nitrogen	No data	

(Continued)

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
Arrow No. 15 (II-C, II-B)	Organic nitrogen	Excretion of dissolved organic nitrogen and exfoliation of particulate organic materials into estuarine sediments from rooted macrophytes not quantified	
II-B Estuarine sediments	Ammonium nitrogen	0.01-0.37 mg NH_3-N/g dry weight sediment (Florida, Waccasassa)	Brooks et al., 1971
	Dissolved free amino acids	Concentration in interstitial water = 350 µg/ℓ (California coast)	Clark et al., 1972
	Ammonium	Concentration in interstitial water (Louisiana): John the Fool Bayou 690 mg/ℓ Airplane Lake 6.45 mg/ℓ	Ho and Lane, 1973
	Free α amino acid-N	John the Fool Bayou 4.13 mg/ℓ Airplane Lake 7.33 mg/ℓ	Ho and Lane, 1973
	Combined amino acid-N	John the Fool Bayou 4.63 mg/ℓ Airplane Lake 2.46 mg/ℓ	Ho and Lane, 1973
	Total N	John the Fool Bayou 17.66 Airplane Lake 18.82	Ho and Lane, 1973
	Total nitrogen	0.39%	Ho, 1971
	Within sediment nitrogen fixation	3.7 g N:m^2:yr Waccasassa Estuary, Florida	Brooks et al., 1971
		113 mg N:m^2:yr - comparative freshwater rate, Lake Mize	Keirn and Brezonik, 1971
		4.9×10^{-3} mg N:9 sed:yr @ 20°C - comparative marine rate - Pacific Ocean	Maruyama et al., 1973
II-C Periphyton and rooted macrophytes	Organic nitrogen	No data on nitrogen contents of benthic algae and rooted macrophytes	
II-D Dissolved mineral pool	Dissolved inorganic nitrogen (total inorganic N)	17.71 µg N/ℓ Pamlico River Estuary 0.315 mg N/ℓ John the Fool Bayou 0.200 mg N/ℓ Airplane Lake 0.13 mg N/ℓ Lake Palourde	Harrison, 1973 Ho et al., 1970
	Ammonium-l	389 µg N/ℓ polluted zone, Scheldt Estuary, Belgium	Billen, 1974
		6.65 µg N/ℓ Pamlico River Estuary 220 µg N/ℓ Lake Mize, Florida, comparative freshwater value	Harrison, 1973 Keirn and Brezonik, 1971
	Nitrate-N	21 µg N/ℓ Scheldt Estuary, Belgium 10.97 µg N/ℓ Pamlico River Estuary 0.09 µg N/ℓ Pamlico River Estuary	Billen, 1974 Harrison, 1973
	Organic nitrogen dissolved free amino acid	115 µg N/ℓ surface waters, coastal California 170 µg N/ℓ - bottom waters, coastal California	Clark et al., 1972
		$\approx 10^{-5}$ m/ℓ sea water $10^{-4} - 10^{-5}$ m/ℓ inshore water	Stephans, 1967
	Total organic nitrogen	0.96 mg N/ℓ , Lake Mize, Florida, comparative freshwater value	Keirn and Brezonik, 1971
Arrow No. 17 (II-B, II-D)	Nitrate nitrogen	0.14 µg N/m^2/sec flux from sediment to water in a nitrification zone, Scheldt Estuary, Belgium	Billen, 1974
	Organic nitrogen	No data	
Arrow No. 17 (II-D, II-B)	Organic and inorganic nitrogen	No data	
Arrow No. 18 (II-D, II-E)	Nitrate-nitrogen	Nitrate Half-Saturation Values:	Carpenter and Guillard, 1971

Cyclotella nana	µg NO_3ℓ	µg N/ℓ
3H	115.94	26.18
7-15	73.78	16.66
13-1	23.56	5.23
Fragilaria pinnata		
13-3	38.44	8.68
0-12	101.68	22.96
Bellerochia sp.		
SD	15.50	3.50
675D	7.44	1.68
Sag-7	425.94	96.18

(Continued)

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
	Ammonium and Nitrate-N	Ammonium and nitrate nitrogen half-saturation values:	

		NO_3-N(μgN/ℓ)	NH_4-N(μgN/ℓ)	
				Eppley et al., 1971
	Ditylum brightwelli	8.40	15.40	
	Coscinodiscus lineatus	33.60 39.20	39.20 16.80	
	Coscinodiscus wailerii	29.40 71.40	60.20 77.00	
	Asterionella japonica	9.80 18.2	21.00 8.4	
	Gonaulox polyedra	120.40	79.80	
	Gymnodinium splendens	53.20	15.40	
	Inorganic nitrogen ammonium	5.7×10^{-3} μg N:ℓ:day mean uptake for mixed plankton sample		Dugdale and Goering, 1967
	Ammonium plus nitrate	Average nitrate uptake with ammonium in the same water = 8.3% (4.7×10^{-4} μg N:ℓ:day) Half-saturation constants (μmoles/ℓ) at 18°C for cultured marine phytoplankton		

	Oceanic species	μg NO_3-N ℓ	μg NH_4-N ℓ	
				Eppley et al., 1971
	Coccolithus huxleyi	1.4	1.4	
	Chaetoceros gracilis	4.2, 1.4	7.0, 4.2	
	Cyclotella nana	4.2, 9.8	5.6	
	Skeletonema costatum	7, 5.6	50.40, 11.20	
	Leptocylindrus danicus	18.2, 16.8	47.6, 12.6	
	Rhizosolenia stolterfothii	49, 35	78.4, 130.2	

		NO_3-N(μgN/ℓ)	NH_4-N(μgN/ℓ)	
	Monochrysis lutheri	8.4	7.0	Eppley et al., 1971
	Isochrysis galbana	1.4	--	
	Dunaliella tertiolecta	19.60	1.4	
II-E Phytoplankton	Organic nitrogen	No fixation of nitrogen in the tidal water column. Flax Pond, Long Island	Whitney et al., 1975
	Aphanizomenon flos-aquae	Nitrogen fixation by blue-green algae in fresh water = 1.8 g:m^2:yr	Horne and Goldman, 1972
	Anabaena circinalis		
	Total nitrogen	1 - 10% of dry weight of cells = 0.16 - 1.6 mg N/ℓ	Fowden, 1962
II-F Detritus microbial decomposers	Organic nitrogen Juncus Roemerianus leaves	During 36-day incubation period, particulate detritus decomposed 50 percent while relative nitrogen content increased from 0.44 to 1.21 percent	de la Cruz and Gabriel, 1974
Arrow No. 19 (II-E, II-G)	Organic nitrogen	No data	
Arrow No. 20 (II-C, II-G)	Organic nitrogen	No data	
Arrow No. 21 (II-C, II-F)	Organic nitrogen	No data	
Arrow No. 22 (II-E, II-F)	Organic nitrogen	No data	
II-G Herbivores	Organic nitrogen	No data on nitrogen content of herbivore populations	
II-H Detritivores	Organic nitrogen	No data on nitrogen content of detritivore populations	
Arrow No. 23 (II-G, II-I)	Organic nitrogen	No data	
Arrow No. 24 (II-F, II-H)	Organic nitrogen	No data	
Arrow No. 24 (II-F, II-H)	Organic nitrogen	No data	
Arrow No. 25 (II-H, II-I)	Organic nitrogen	No data	
Arrow No. 26 (II-I, II-B)	Organic nitrogen	No data	
Arrow No. 27 (II-G, II-F)	Organic nitrogen	No data	
Arrow No. 28 (II-D, II-F)	Organic and inorganic nitrogen	No data	
Arrow No. 28 (II-F, II-D)		No data	
Arrow No. 29 (II-D, II-H)	Organic and inorganic nitrogen	Does not occur	
Arrow No. 29 (II-H, II-D)	Organic nitrogen	Urea excretion not determined for populations of detritivores	
Arrow No. 30 (II-D, II-I)	Organic and inorganic nitrogen	Does not occur	

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(Continued)

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
Arrow No. 30 (II-I, II-D)	Organic nitrogen	Urea excretion not determined for populations of carnivores	
II-I Carnivores	Organic nitrogen	Nitrogen content not studied for populations of carnivores	
Arrow No. 31 (II-G, II-D)	Organic and inorganic nitrogen	Does not occur	
	Organic and inorganic nitrogen	Urea and ammonium excretion not determined for populations of herbivores	
Arrow No. 32 (II-A, II-B)	Organic and inorganic nitrogen	No data on nitrogen removal to sediments either sorbed to precipitating materials or as a component of them	
Arrow No. 33a-e	Organic nitrogen	No data on nitrogen removal to sediments in the form of dead organisms	
Arrow No. 34 (II-F1, II-F2)	Total inorganic nitrogen	Average release of total inorganic nitrogen accompanying decomposition of mixed plankton = 0.067 µg N/ℓ/day^{-1}	Ryther and Dunstan, 1971
Arrow No. 34 (II-F2, II-F1)	Organic nitrogen	No data	
Arrow No. 35A (II, I)	Organic nitrogen	Nitrogen contained in detritus is reshuffled by tides that move the material around on the marsh. Amount of nitrogen so affected not measured	
	Nitrate nitrogen	1.3 kg N/tide. Flax Pond, Long Island	Whitney et al., 1975
Arrow No. 35B (I&III, II)	Organic nitrogen		
	Nitrate nitrogen	5.4 kg N/tide - Flax Pond, Long Island	Whitney et al., 1975
Arrow No. 36 (II-A, III)	Organic nitrogen	Organic nitrogen moving upstream as fish not assessed	
Arrow No. 36 (III, II-A)	Total inorganic nitrogen	Average nitrate plus ammonia input of river water estimated from U. S. Geological Survey water resources data = 0.1 mg Nℓ^{-1}	Haines, 1975
	Organic nitrogen	No data	
Arrow No. 37 (I, IV)	Inorganic nitrogen (molecular and nitrous oxide)	Loss up to 17% of total nitrogen in 120 days	Patrick and Gotoh, 1974
		7.64 ppm NO$_3$-N/day microbial NO$_3$ removal from floodwater over salt marsh	Engler and Patrick, 1974
	Inorganic nitrogen (molecular and nitrous oxide) (Continued)	One-half to two-thirds of labelled N lost during 4 months of incubation. Fifteen to 20% of total soil nitrogen lost as a result of alternate submergence and drying	Patrick and Tusneem, 1972
Arrow No. 37 (IV, I)	Inorganic nitrogen	Nitrogen fixation rates	
	Marsh soils	Top 4 cm of all sediments	Whitney et al., 1975
		12-800 µg N:m^2:hr^{-1} - Flax Pond, Long Island	
	Stagnant pools	8.6-4800 µg N:m^2:hr - Flax Pond, Long Island	
	Panne	63.5 µg N:m^2:hr - Flax Pond, Lond Island	
	Mudflat	136.0 µg N:m^2:hr - Flax Pond, Long Island	
	Spartina sediments		
	Tall form	116.0 µg N:m^2:hr	Whitney et al., 1975
	Dwarf form	65.1 µg N:m^2:hr	
	Inorganic nitrogen	Fixation by algae on marsh soil	Van Raalte et al., 1974
		surface - mg N:m^2:hr	
		June 1972 - 159.5 - Massachusetts August 1972 - 12.13 - Massachusetts May 1973 - 97.7 - Massachusetts June 1973 - 161.3 - Massachusetts	
		Blue-green algae mats - 59.9 µg N:cm^2:hr - Massachusetts	
		Blue-green algae mats - 260-8900 µg N:m^2:hr^1 - Flax Pond, Massachusetts	Whitney et al., 1975
	Organic nitrogen	No data on nitrogen content of marsh algae	
Arrow No. 38 (II-A, IV)	Molecular nitrogen estuarine water	No data	
Arrow No. 38 (IV, II-A)	Molecular nitrogen atmosphere	No data	
Arrow No. 39A (V, II)	Organic and inorganic nitrogen in estuary waters	No data	
Arrow No. 39B (II, V)	Organic and inorganic nitrogen in ocean waters	No data	

Table A16

Cycling of Phosphorus in Marsh-Estuarine Ecosystems as Described by the General Compartmental Model

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
I-A Marsh soil	Total phosphorus in soil	Saline vegetative type of soil, average of 0.08 ppt. Brackish vegetative type of soil, average of 0.004 ppt. Both from the Louisiana Gulf coast	Chabreck, 1972
Arrow No. 1 (I-A, I-B)	Inorganic phosphorus	Label in soil moves into plant in maximum concentration in 10-15 days post-addition	Reimold, 1972
Arrow No. 1 (I-B, I-A)	Organic phosphorus	No data on amount of organic phosphorus excreted by grass roots or organic phosphorus lost to soil by sloughing of root and rhizome tissues	
Arrow No. 2 (I-A, I-C)	Inorganic phosphorus	No data	
Arrow No. 2 (I-C, I-A)	Organic phosphorus	No data	
I-B Marsh grasses	Phosphorus in marsh grasses	Percent phosphorus content	
	Spartina alterniflora	0.25 - Georgia marshes	Burkholder, 1956
	Spartina cynosuroides	0.10 - Gulf coast marshes	de la Cruz, 1973
		0.14 - Atlantic coast marshes	Johnson, 1970
	Spartina patens	0.04 - Louisiana coastal marshes	Chabreck, 1972
	Juncus roemerianus	0.24 - Gulf coast marshes	de la Cruz, 1973
	Distichlis spicata	0.11 - Louisiana coastal marshes	Chabreck, 1972
	Scirpus robustus	0.08 - Louisiana coastal marshes	Chabreck, 1972
Arrow No. 3 (I-B, I-E)	Organic phosphorus	No data	
Arrow No. 4 (I-B, I-D)	Organic phosphorus	No data	
I-C Soil and epiphytic algae	Total phosphorus	Phosphorus content (Note: examples are mainly freshwater phytoplanktons)	
	Asterionella formosa	6×10^{-8} to 4×10^{-6} µg P/cell	Lund, 1950
	Algae in general	Minimum phosphorus requirement in culture experiments 6×10^{-8} µg P/cell	Mackereth, 1953
	Asterionella japonica	5×10^{-8} µg P/cell	Goldberg et al., 1951
	Chlorella pyrenoidosa	Minimum content = 1×10^{-7} µg P/cell Maximum content = 1.5×10^{-6} µg P/cell	Al Kholy, 1956
	Scendesmus quadricanda	9.2×10^{-7} µg P/cell - 8.7×10^{-6} µg P/cell	Franzew, 1932
Arrow No. 5 (I-C, I-D)	Organic phosphorus	No data	
Arrow No. 6 (I-C, I-E)	Organic phosphorus	No data	
Arrow No. 7 (I-D, I-G)	Organic phosphorus	No data	
Arrow No. 8 (I-D, I-E)	Organic phosphorus	No data	
Arrow No. 9 (I-F, I-E)	Organic phosphorus	No data	
Arrow No. 9 (I-E, I-F)	Organic phosphorus	No data	
Arrow No. 10 (I-F, I-G)	Organic phosphorus	No data	
Arrow No. 11 (I-G, I-E)	Organic phosphorus	No data	
I-F Detritivores	Organic phosphorus	No data	
Arrow No. 12 (I-E1, I-E2)	Organic phosphorus	No data	
Arrow No. 12 (I-E2, I-E1)	(Particulate and dissolved)	No data	
I-E (1 and 2) Detritus-microbial decomposers	Organic phosphorus (particulate and dissolved)	No data	
Arrow No. 13 (I-E, I-A)	Organic phosphorus	No data	
Arrow No. 13 (I-A, I-E)	Organic phosphorus	No data	
Arrow No. 14 (I-B, I-E)	Organic phosphorus	No data	
I-G Carnivores	Organic phosphorus	No data	

(Continued)

* Fresh water.
** 8 µg-atoms P/ℓ originally in water.

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Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
Arrow No. 15 (II-B, II-C)	Inorganic phosphorus	From interstitial water in root zone into eelgrass - 0.34 µg P/plant	McRoy and Barsdate, 1970
		Sediment phophorous sorption by _Myrio-phyllum exalbescens_ (fresh water, milfoil)	DeMarte and Hartman, 1974
		Muck - 911 cpm:g dry weight:8 hr	
		Sand - 14,016 cpm:g dry weight:8 hr	
Arrow No. 15 (II-C, II-B)	Organic phosphorus	No data on amount of organic phosphorus lost by plants by excretion into sediments or by sloughing of roots and rhizomes	
II-B Estuarine sediment	Available phosphorus		
II-B - Estuary sediment	Available phosphorus	Freshwater sediment = 1.6 µg P/g of sediment	Upchurch et al., 1974
		18 ppt salinity sediment = 0.3 µg P/g of sediment	
		Both from Pamlico Estuary	
	Total phosphorus	Data available for freshwater mud only	Harter, 1968
	Total phosphorus	230 mg/100 g mud	
	NH_4-F soluble P	19 mg/100 g mud	
	NAOH soluble P	27 mg/100 g mud	
II-C Periphyton and rooted macrophytes	Organic phosphorus	No data available for individual species of macrophytes. For examples of data on various algae, see Compartment I-C, Soil and Epiphytic Algae, this section	
II-D Dissolved mineral pool	Dissolved and particulate phosphorus Dissolved Inorganic phosphorus	Halifax, Nova Scotia, coastal waters Percent of total and equivalent amounts 0.9% = 0.35 µg-atoms P/ℓ	Watt and Hayes, 1963
	Particulate phosphorus	75.8% = 2.98 µg-atoms P/ℓ	
		15.3% = 0.60 µg-atoms P/ℓ	
	Interconversion rates	Between dissolved inorganic phosphorus and particulate phosphorus 0.23 µg-atoms P:ℓ:day	
		Between particulate phosphorus and dissolved organic phosphorus 1.2 µg-atoms P:ℓ:day	
	Normal phosphate	0.23-0.29 µg P/ℓ Georgia estuaries	Pomeroy et al., 1965
	Phosphorus in estuarine water	1.25 µg P/ℓ Sapelo Island, Georgia	Pomeroy, 1960
	Brackish seawater	2.9 µg at P/ℓ (30% salinity)	Ketchum, 1967
	Surface coastal water	0.5 µg at P/ℓ (30.95% salinity)	
	Deep ocean water	1.25 µg at P/ℓ (34% salinity)	
Arrow No. 17 (II-B, II-D)	Inorganic phosphorus	Phosphorus in Equilibrium Between Sediment and Water (Fresh Water)	MacPherson et al., 1958

pH	Acid Bog Lake	Productive Lake	Medium Lake	Unproductive Lake
4	0.17 mg/ℓ	0.25	0.05	0.025
5	0.15 mg/ℓ	0.22	0.05	0.05
6	0.17 mg/ℓ	0.20	0.075	0.075
7	0.2 mg/ℓ	0.18	0.15	0.125
8	0.3 mg/ℓ	0.30	0.35	0.2

Extractable phosphorus from submerged soil	10-35 ppm, depending on redox potential, +500+ +200 mV		Patrick, 1964
Phosphorus release to water*	Final Concentration of Phosphorus (ppm)		Patrick, 1964

	pH	Aerobic	Anaerobic
Commerce soil	5.4	0.02	2.92
Crowley soil	6.1	0.002	0.005
Moreland soil	6.8	0.14	4.48
Sharkey soil	6.5	0.03	1.17

(Continued)

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage			Reference

Arrow No. 17 (II-B, II-D) and (II-D, II-B)	Phosphate-phosphorus equilibrium between estuarine water and sediments	Initial Concentration of Phosphate in water ($\mu g/\ell$)	Final Concentration of Phosphate in water ($\mu g/\ell$)	Change in Phosphate Concentration in Sediments ($\mu g\ PO_4/g$ dry Sediment)	Pomeroy et al., 1965
		0	0.72 ± 0.03	-1.0	
		0.5	0.73 ± 0.02	-0.4	
		1.0	0.90 ± 0.07	+0.6	
		2.5	0.89 ± 0.05	+7.6	
		4.3	0.87 ± 0.02	+11.0	
		8.4	1.61 ± 0.22	+30.9	

Arrow No. 17 (II-D, II-B)	Phosphorus uptake from water (fresh)	100 mg/mℓP added to water, Final P Concentration in Water (mg/mℓ)			Patrick, 1964
			Aerobic Conditions	Anaerobic Conditions	
		Commerce soil	79.2	66.1	
		Crowley soil	40.8	6.7	
		Moreland soil	48.2	13.0	
		Sharkey soil	62.7	14.0	

Arrow No. 18 (II-D, II-E)	Inorganic phosphorus	0.511 g/m^{2}P required to maintain primary production of 2 gC:m^2:day	Ketchum and Corwin, 1965
Arrow No. 18 (II-E, II-D)	Organic phosphorus	0.507 g:m^2:day phosphorus excreted by plankton to water	Ketchum and Corwin, 1965
	Organic and inorganic phosphorus	8.1 μg-at P:g algae:hr excreted by algae into water	Satomi and Pomeroy, 1965
II-E Phytoplankton	Organic phosphorus	For examples of data on the various algae, see Compartment I-C, Soil and Epiphytic Algae, this section	
II-F Detritus-microbial decomposers	Organic phosphorus (dissolved and particulate)	No data	
Arrow No. 19 (II-E, II-G)	Organic phosphorus	Fresh water data only: Particulate food (algae and bacteria) ingested by zooplankton	Peters and Rigler, 1973
		27.4% of total phosphorus of trophogenic zone ingested/day	
		54% of ingested materials are assimilated	
		Most of the assimilated phosphorus is excreted as PO$_4$	
		46% of ingested phosphorus defecated in particulate form	
		10.6% of total trophogenic zone phosphorus regenerated/day	
		Phosphorus content of yeast ingested by Daphnia rosea = 8.97 μg P/day	Peters and Lean, 1973
Arrow No. 20 (II-C, II-G)	Organic phosphorus	No data	
Arrow No. 21 (II-C, II-F)	Organic phosphorus	No data	
Arrow No. 22 (II-E, (II-F)	Organic phosphorus	No data	
Arrow No. 23 (II-G, II-I)	Organic phosphorus	No data	
II-G Herbivores	Organic phosphorus	No estimates available for phosphorus content of total herbivore population	
II-H Detritivores	Organic phosphorus	No estimates available for phosphorus content of total detritivore population	
Arrow No. 24 (II-F, II-H)	Organic phosphorus	2.4-8.2 mg P/m^2	Pomeroy et al., 1972
Arrow No. 25 (II-H, II-I)	Organic phosphorus	No data	
Arrow No. 26 (II-I, II-F)	Organic phosphorus	No data	
Arrow No. 27 (II-G, II-F)	Organic phosphorus	No data	
Arrow No. 28 (II-D)	Inorganic phosphorus	Lake water to particulate fraction ≈ 0.9 min	Lean, 1973
		Lake water to colloid fraction (binding) = 0.022/min	

(Continued)

Table A16 (Concluded)

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
	Dissolved inorganic phosphorus (DIP)	Estuarine water to protozoan:	Johannes, 1965

DIP remaining in water after (µg atoms/ℓ)

Organism	1 day	7 day
Euplotes vannus	0.18	3.1
Ciliate #11	0.11	2.0
Ciliate #13	0.11	2.0
Mixed ciliates	0.21	4.0
Ciliate #2	0.08	6.0
Ciliate #4	0.23	4.5
Ciliate #6	0.17	3.8
Ciliate #14	0.16	2.1
Bacterial control	0.19	0.6

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
Arrow No. 28 (II-F, II-D)	Organic phosphorus	Particulate fraction to lake water = 0.022/min	Lean, 1973
		Colloid fraction to lake water = 0.0017/min	
		Phosphorus excretion rates (body equivalent contents)	**Johannes, 1965**

Euplotes crassus	160 min
Euplotes vannus	20 min
Euplotes trisulcatus	43 min
Uronema sp.	14 min

Bacteria to protozoa to water - 9-10 days of turnover time (31-85% of dissolved inorganic phosphorus concentration)

Bacteria to water - 9-10 days of turnover time (<1% of phosphorus in culture)

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
Arrow No. 29 (II-D, II-H)	Inorganic phosphorus	Does not occur	
Arrow No. 29 (II-H, II-D)	Inorganic phosphorus	Phosphorus excretion data:	
	Oysters	0.2 ± 0.03 µg-atoms P/g/hr spring 0.2 ± 0.06 µg-atoms P/g/hr summer	Satomi and Pomeroy, 1965
	Detritus feeders	2.4-8.2 mg/m²	Pomeroy et al., 1972
Arrow No. 30 (II-D, II-I)	Inorganic phosphorus	Does not occur	
Arrow No. 30 (II-I, II-D)	Inorganic and organic phosphorus	Excretion by *Fundulus* and *Notemigonus* to water - 2 cpm/gP in organism	Coffin et al., 1949
Arrow No. 31 (II-D, II-G)	Inorganic phosphorus	Does not occur	
Arrow No. 31 (II-G, II-D)	Inorganic and organic phosphorus	Excretion by zooplankton to water 7.9 ± 0.8 µg-atoms P:g:hr	Satomi and Pomeroy, 1965
	Orthophosphate phosphorus	Excretion by zooplankton to water 950 µg-atoms P:m³:day = 4.71 mg P:g dry plankton:day	Pomeroy et al., 1963
	Soluble organic phosphorus	Excretion by zooplankton to water 882 µg-atoms P:m³:day = 4.55 mg P:g dry plankton:day	Pomeroy et al., 1963
	Inorganic phosphorus	Excretion by *Daphnia rosea* to water (fresh):	Peters and Lean, 1973
		Rate ~ 0.08 µg P:mg dry weight:hr Net - 0.823 µg P:mg dry weight	
Arrow No. 32-34 and 36-40 (All Compartments)	Organic and inorganic phosphorus	No data	
Arrow No. 35A (II, I)	Dissolved phosphorus (organic and inorganic)	No data on uptake from waters by salt marshes	
Arrow No. 35B (I, II)	Dissolved inorganic phosphorus*	Excretion by marsh grasses into tidal waters = 9.84 mg-atoms P/m/(tidal cycle)	Reimold, 1972

* General Turnover Times for Inorganic Phosphorus in Georgia Coastal Waters

Doboy Sound	50 hr light, 69 hr dark (February)	Pomeroy, 1963
Doboy Inlet	4 hr light or dark (April)	
Coastal water	34 hr light, 73 hr dark (April)	
Sapelo salt marsh water	11 hr light, 49 hr dark	
Altamaha River (Nostoceae bloom)	1 hr light, 9 hr dark (May)	

(Sheet 4 of 4)

Table A17

Cycling of Sulfur in Marsh-Estuarine Ecosystems as Described by the General Compartmental Model

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
I-A Marsh soil	Inorganic sulfur Sulfides-sulfates Organic sulfur	Oxidation of inorganic sulfide Rapid in soil under aerobic conditions *One-half of sulfide oxidized in 15 min* All sulfide oxidized in 18 hr	Connell and Patrick, 1969
		Reduction of sulfate requires **redox < -150 mV**	
Arrow No. 1 (I-A, I-B)	Inorganic sulfur*	Uptake of inorganic sulfides by rice plants in flooded soil:	Engler and Patrick, 1975

	Solubility Product Constant (Ksp)	Percent Uptake of Added S =
Na_2S	1.0×10^{-1}	4.49
MnS	1.4×10^{-15}	0.62
FeS	3.7×10^{-19}	0.43
ZnS	1.2×10^{-23}	0.38
CuS	3.5×10^{-38}	0.18
HgS	1.0×10^{-50}	0

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
Arrow No. 1 (I-B, I-A)	Organic sulfur	No data	
I-B Marsh grasses	Total (organic sulfur)		
	Spartina alterniflora	Percent total content (North Carolina)	Broome et al., 1973
	Tall form Short form	0.48 0.75	
II-B Estuarine sediment	Sulfide-sulfur	*Sulfide production in 10 cm. Mud cores* from fresh water:	Ivanov, 1968
		0.5-1.5 mg $S^=$:(kg wet sediment)$^-$:(day) deepest part of lake	
		12-19 mg $S^=$:(kg wet sediment)$^-$:(day) slope of lake	
		Sulfide production in laboratory mixed cultures containing sulfate reducing bacteria: 10-45 mg $S^=$:ℓ$^-$:day	Nakai and Jensen, 1964
Arrow No. 28 (II-F, II-D)	Sulfide-sulfur	Production of sulfide in detritus mixtures: 10-45 mg $S^=$ℓ$^{-1}$:day by decomposition of algal extracts and sediments	Ranim and Bella, 1974
	Sulfide-sulfur	Production of sulfide by sediment bacteria:	Edwards, 1967
		Desulfovibrio desulfuricans - pure batch cultures	
		Growing populations 200-250 mg $S^=$:ℓ$^-$:day	
		Stable populations 100-150 mg $S^=$:ℓ$^-$:day	
		Field determination in lake water using ^{35}S: 0.1-0.2 mg $S^=$:ℓ$^-$:day	Sorokin, 1970
		In muds collected from slope of lake near river mouth: 10-15 mg $S^=$:(kg wet sediment)$^-$:day	

No other data

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* This and preceding sulfides were unstable in aerobic soil with degree of oxidation of sulfide by oxygen in soil adjacent to root zones responsible for making sulfur accessible for uptake.

Cycling of Lead in Marsh-Estuarine Ecosystems as Described by the General Compartmental Model

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
I-A Marsh soil	Total lead	Mean lead contents in top 2 cm of marsh soil:	Banus et al., 1975
		72.8 mg/m^2 (1971) 72.5 mg/m^2 (1972) Great Sippewisset Salt Marsh, Massachusetts	
		Mean lead contents in top 2 cm of marsh soil fertilized with low levels of fertilizer:	
		74.0 mg/m^2 (1971) 120.0 mg/m^2 (1972)	
		Mean lead contents in top 2 cm of marsh soil fertilized with high levels of fertilizer:	
		131 mg/m^2 (1971) 157 mg/m^2 (1972)	
		Lead contents of marsh soil of dredged material origin (ppb) 26.0 ppb - Virginia	Driffmeyer and Odum, 1974
		Average metal contents in upper 40 cm [μg (g dry weight of sediment)$^{-1}$]	Dunstan and Windom, 1975
		22.2 Santee River 13.9 Cooper River 15.9 Savannah River 19.2 Altamaha River 14.0 Satilla River 9.4 St. Johns River Average content 16.6 Georgia salt marsh estuaries	
		Range of lead in marsh soil 0.5-20 ppm	Dunstan et al., 1975
	Total lead in various layers of soil	Average contents in ppm of soil dry weight	Hallberg, 1974
	A layer B layer C layer D layer	9.51 ppm Denmark 7.58 ppm 15.56 ppm 1.92 ppm	
	Acid-soluble fraction	Top 2 cm of marsh soil cores Control plots 62.3 ± 2.1 ppm LF plots 113.0 ± 5.0 ppm HF plots 117.0 ± 22.7 ppm Great Sippewisset Salt Marsh, Massachusetts	Valiela et al., 1974
	Total lead	Lead in Connecticut salt marshes in ppm	Siccama and Porter, 1972

		Surface	1 m deep
Area 1		107 ± 7	30 ± 5
Area 2		95 ± 5	13 ± 2
Area 3		83 ± 5	31 ± 6
Area 4		82 ± 4	10 ± 3
Means		92	21

Quantitative distribution in 3 soil profiles — Siccama and Porter, 1972

	cm	g/m^2	Total, %
Pit No. 1	0-23	3.6	53
	23-33	1.8	26
	33-119	1.5	21
Pit No. 2	0-9	2.8	36
	9-38	2.3	30

(Continued)

Note: LF--from areas treated with low levels of fertilizer.
      HF--from areas treated with high levels of fertilizer.

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Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage			Reference
I-A Marsh soil		cm	g/m^2	Total, %	
	Pit No. 2 (Continued)	38-117	0.9	12	
		117-140	1.7	22	
			7.7		
	Pit No. 3	0-19	1.5	29	
		19-25	0.2	4	
		25-51	0.4	8	
		51-81	0.5	10	
		81-89	0.2	4	
		89-163	2.3	45	
		Average	5.1		
		Average Cone	6.5 ppb		

	Total lead	Concentration of lead in sediment cores from areas where _Spartina alterniflora_ was growing:	Banus et al., 1974
		0-10 cm 912.5 ppm Neponset River Marsh 60 cm 15.5 ppm	
		0-10 cm 98.1 ppm Barnstable River Marsh 10-13 cm 38.8 ppm	
		0-2 cm 66.0 ppm Great Sippewissett 9-10 cm 50.0 ppm Marsh 15-16 cm 63.0 ppm	
I-B Marsh grasses	Total lead _Spartina alterniflora_	Mean lead content of live and dead plants (ppm of oven-dried materials)	Banus et al., 1975
	Live plants	1971 Control 6.8 ppm LF 9.8 ppm HF 12.3 ppm	
		1972 Control 2.3 ppm LF 3.2 ppm HF 4.8 ppm	
	Dead plants	1972 Control 10.8 ppm HF 10.3 ppm	
	Spartina patens		
	Live plants only	1971 Control 5.8 ppm LF 7.8 ppm HF 7.8 ppm	
		1972 Control 2.6 ppm LF 1.8 ppm HF 5.0 ppm	
		Comparative lead levels in grasses on natural and dredged material soils in ppm/g (dry weight of grass)	Driffmeyer and Odum, 1974

	Dredged Material	Natural Marsh
Phragmites communis	4.4 + 5.3	0.5 + 0.6
Spartina alterniflora	5.1 + 1.2	1.9 + 0.7
Spartina patens	9.1 + 2.9	0.8 + 1.4

Average contents: 14.0 ppm for grasses on dredged material, 2.0 ppm for grasses on natural soils

Average lead concentrations in _Spartina alterniflora_ from several Georgia area salt marsh estuaries in µg/(g dry weight of aboveground and rhizome)   Dunstan and Windom, 1975

5.35 Santee River
4.2 Cooper River

(Continued)

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
I-B Marsh grasses (Continued)	Total lead Spartina alterniflora (Continued)	5.2 Savannah River 4.2 Altamaha River 2.6 Satilla River 2.83 St. Johns River Average 4.06 µg/g Concentration in live plant samples:	Banus et al., 1974
	Spartina alterniflora	23.2 ppm Neponset Marsh 5.4 ppm Barnstable Marsh 6.8 ppm Great Sippewissett Marsh Average 13.2 -- values from several Massachusetts salt marshes	
II-E Detritus-microbial decomposers	Total lead	Mean concentration of lead in detritus from tidal creek sediments: 1972 Control 77 ppm LF 62 ppm HF 106 ppm Concentration in detritus from dredged material grown plants: 11.5 ppm	Banus et al., 1975 Driffmeyer and Odum, 1974
	Acid-soluble lead	Concentration in acid-soluble fraction of detritus on marsh creek surfaces: Control 77.3 ppm LF 105.8 ppm HF 65.3 ppm Great Sippewissett Salt Marsh, Mass.	Valiela et al., 1974
I-F Marsh detritivores	Total lead Modiolus demissus	Averages for 2 yr (1971-1972): Control 2.7 ppm LF 3.1 ppm HF 2.6 ppm	Banus et al., 1975 Valiela et al., 1974
	Uca pugnax	Control 0.7 ppm LF 3.0 ppm HF 7.5 ppm	
II-B Estuarine sediments	Total lead	Fresh water example: Ottawa River 26 ppb Rideau River 42 ppb Suspended estuarine sediment: 82 µg/(g dry weight of sediment) Suspended sediment entering estuary from river: 87 µg/(g dry weight of sediment) Above are averages for southeast coastal marsh-estuaries	Oliver, 1973 Dunstan and Windom, 1975

(Continued)

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
II-B Estuarine sediments (Continued)	Methyl lead	Methylation of lead in aquatic sediments (no estuarine studies to date; all fresh water)	Wong et al., 1975
		Trimethyl lead to tetramethyl lead – 6 percent/week	
II-C Periphyton and rooted macrophytes	Total lead *Macrocystis pyrifera*	Average concentration in µg/(g ash weight) = 6.5 ± 1.6	Boothe and Knauer, 1972
II-D Dissolved mineral pool	Soluble lead	1.5 ppb in water 2.2 ppb in estuarine water 2.3 ppb in river water (via Arrow No. 36 III, IIA) Above are averages for southeast area marsh-estuaries	Dunstan et al., 1975
		Average concentrations during various times of year, Monterey Bay, California: Period of intense coastal upwelling = 1 µg/ℓ Period of low upwelling = 0.5 µg/ℓ Period of oceanic dominance = 0.4 µg/ℓ Period of mixing = 1.8 µg/ℓ Average value for Pacific Ocean = 0.4 µg/ℓ	Knauer and Martin, 1973
II-E Phytoplankton	Total lead	Pond ecosystems in salt marshes established on dredged material: 29.0 ppm (Virginia)	Driffmeyer and Odum, 1974
		Phytoplankton in Monterey Bay, California: Period of intense upwelling = 5 µg/ (g dry weight) Period of low upwelling = 5 µg/(g dry weight) Period of oceanic dominance = 10 µg/(g dry weight)	Knauer and Martin, 1973
II-G Herbivores	Total lead	Herbivores in pond ecosystems in salt marshes established on dredged material (Virginia)	Driffmeyer and Odum, 1974
	Cyprinodon varigatus *Gambusia affinis*	3.3 ppm 8.4 ppm	
II-H Detritivores	Total lead *Palaemonetes pugio* (shrimp)	Detritivores in pond ecosystems in salt marshes established on dredged material: 11.0 ppm	Driffmeyer and Odum, 1974
	Mercenaria mercenaria (clam)	2.8 ± 0.6 ppm	Valiela et al., 1974
	Crassostrea virginica (oysters)	<1 ppm	
II-I Carnivores	Total lead	Carnivores in pond ecosystems in salt marshes established on dredged material: 4.5 ppm	Driffmeyer and Odum, 1974

Table A19

Cycling of Zinc in Marsh Estuarine Ecosystems as Described by the Marsh-Estuarine Model

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
I-A Marsh soil	Total zinc	Mean zinc contents in top 2 cm of marsh soil:	Banus et al., 1975
		$\quad$ 102.0 mg/m^2 (1971)	
		$\quad$ 142.0 mg/m^2 (1972)	
		Great Sippewissett Salt Marsh, Mass.	
		Mean zinc contents in top 2 cm of marsh treated with low levels of fertilizer:	
		$\quad$ 158 mg/m^2 (1971)	
		$\quad$ 249 mg/m^2 (1972)	
		Mean zinc contents in top 2 cm of marsh treated with high levels of fertilizer:	
		$\quad$ 107 mg/m^2 (1971)	
		$\quad$ 682 mg/m^2 (1972)	
		Average zinc concentrations in marsh soils from Southeastern Salt Marsh-Estuaries in µg/(g dry weight of sediment)	Dunstan and Windom, 1975
		$\quad$ 69.0 $\quad$ Santee River	
		$\quad$ 42.4 $\quad$ Cooper River	
		$\quad$ 69.6 $\quad$ Savannah River	
		$\quad$ 44.2 $\quad$ Altemaha River	
		$\quad$ 43.3 $\quad$ Satilla River	
		$\quad$ 14.9 $\quad$ St. Johns River	
		$\quad$ 49.8 $\quad$ Average	
		Range of zinc concentrations in upland (New York) soils: 32-172 ppb	Hodgson et al., 1966
	Soluble zinc	Zinc complexed in soil solution in upland (New York) soils: 66 ppb (37%)(silt and gravel loams)	
		Zinc in layers of soil in Danish intertidal area (ppm):	Hallberg, 1974
	Layer A	41.0	
	Layer B	28.9	
	Layer C	43.5	
	Layer D	5.1	
	Soluble zinc	Zinc in phases of soil solution (ppm):	Geering and Hodgson, 1969
		$\quad$ Orginal solution = 0.165 ppm (83%)	
		$\quad$ Nondialyzable soil solution = 0.025 ppm	
		$\quad$ Dialyzable fraction = 0.120 ppm	
	Acid-soluble zinc	Concentration in acid-soluble fraction of top 2 cm of cores:	Valiela et al., 1974
		$\quad$ Control $\quad$ 113.0 $\pm$ 11.6 mg/m^2	
		$\quad$ LF $\quad$ 228.0 $\pm$ 18.6 mg/m^2	
		$\quad$ HF $\quad$ 514.0 $\pm$ 43.5 mg/m^2	
	Total zinc	63.7 ppm dredged spoil (Virginia)	Driffmeyer and Odum, 1974
		6.3 ppm in natural marsh soil	
I-B Marsh grasses	Total zinc Spartina alterniflora Live plants	Mean concentration of zinc in plants from from Great Sippewissett Marsh:	Banus et al., 1975
		$\quad$ Control $\quad$ 1971 $\quad$ 16.5 $\pm$ 2.2 ppm	
		$\quad\quad\quad\quad\quad$ 1972 $\quad$ 10.8 $\pm$ 1.3 ppm	
		$\quad$ LF $\quad\quad\quad$ 1971 $\quad$ 24.2 $\pm$ 3.4 ppm	
		$\quad\quad\quad\quad\quad$ 1972 $\quad$ 13.8 $\pm$ 0.9 ppm	
		$\quad$ HF $\quad\quad\quad$ 1971 $\quad$ 29.3 $\pm$ 2.3 ppm	
		$\quad\quad\quad\quad\quad$ 1972 $\quad$ 26.7 $\pm$ 6.4 ppm	
	Dead plants	$\quad$ Control $\quad$ 1972 $\quad$ 17.0 $\pm$ 1.1 ppm	
		$\quad$ HF $\quad\quad\quad$ 1972 $\quad$ 44.8 $\pm$ 3.8 ppm	
	Spartina patens Live only	$\quad$ Control $\quad$ 1971 $\quad$ 15.3 $\pm$ 3.8 ppm	
		$\quad\quad\quad\quad\quad$ 1972 $\quad$ 11.8 $\pm$ 2.3 ppm	
		$\quad$ LF $\quad\quad\quad$ 1971 $\quad$ 30.5 $\pm$ 6.4 ppm	
		$\quad\quad\quad\quad\quad$ 1972 $\quad$ 12.4 $\pm$ 1.6 ppm	
		$\quad$ HF $\quad\quad\quad$ 1971 $\quad$ 28.6 $\pm$ 5.6 ppm	
		$\quad\quad\quad\quad\quad$ 1972 $\quad$ 19.3 $\pm$ 2.8 ppm	
	Total zinc	Concentration of zinc in grasses occurring in dredge-spoil pond and natural marsh ecosystems in Virginia	Driffmeyer and Odum, 1974

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Dredged Spoil	Natural Marsh	
I-B Marsh grasses (Continued)	Total zinc			
	Phragmites communis	24.8 $\pm$ 6.8 ppm	14.0 $\pm$ 0.3 ppm	
	Spartina alterniflora	38.6 $\pm$ 12.4 ppm	20.1 $\pm$ 1.0 ppm	
	Spartina patens	28.9 $\pm$ 10.2 ppm	21.2 $\pm$ 0.8 ppm	
	Spartina alterniflora	Average zinc concentrations in plants from southeastern salt marsh-estuaries in µg/(g dry weight of sediment)[1]		Dunstan and Windom, 1975
		$\quad$ 33.8 $\quad$ Santee River		
		$\quad$ 36.7 $\quad$ Cooper River		
		$\quad$ 24.6 $\quad$ Savannah River		
		$\quad$ 30.6 $\quad$ Altamaha River		
		$\quad$ 39.8 $\quad$ Satilla River		
		$\quad$ 27.8 $\quad$ St. Johns River		

(Continued)

Note: LF--from areas treated with low levels of fertilizer. HF--from areas treated with high levels of fertilizer.

Table A19 (Concluded)

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
I-E Detritus-microbial decomposers	Acid soluble zinc	Concentration in acid-soluble fraction of detritus on marsh creek surfaces, Great Sippewissett Salt Marsh, Mass.	Valiela et al., 1974
		Control 139.5 ± 23.0 ppm LF 189.0 ± 17.7 ppm HF 239.0 ± 28.0 ppm	
I-F Detritivores	Total zinc	Mean concentration in detritivores from Great Sippewissett Salt Marsh, Mass.	Banus et al., 1975 Valiela et al., 1974
	Modiolus demissus	Control 48 ± 0.9 ppm LF 52 ± 1.4 ppm HF 52 ± 2.0 ppm	
	Uca pugnax	Control 92 ± 3 ppm LF 109 ± 11 ppm HF 81 ± 1 ppm	
II-B Estuarine sediment	Total zinc	Freshwater example:	Oliver, 1973
		Ottawa River 84 ppb Rideau River 86 ppb	
		Concentration of zinc in suspended sediments in Southeastern Salt Marsh-Estuaries (ppb) Sediment of estuarine origin ≈ 471 ppb Sediment of riverine origin (Arrow No. 36 III, IIA) = 496 ppb	Dunstan and Windom, 1975
II-C Periphyton and rooted macrophytes	Total zinc	Concentration of zinc in plant:	
	Macrocystis pyrifera	33 ± 2.2 μg/(g ash dry weight)	Boothe and Knauer, 1972
	Fucus serratus	316 ppm (dry weight average)	Fuge and James, 1973
	Fucus vesiculosus	433 ppm (dry weight average)	
II-D Dissolved mineral pool	Soluble zinc	None found in southeastern salt marsh-estuaries	Dunston and Windom, 1975
		Zinc in water in Monteray Bay, Calif:	Knauer and Martin, 1973
		Period of intense upwelling = 12 μg/ℓ	
		Period of low upwelling = 6 μg/ℓ	
		Period of oceanic dominance = 4 μg/ℓ	
		Period of mixing = 2.7 μg/ℓ	
		Average surface water concentration Pacific Ocean (Hawaii to Monterey) = 2.0 μg/ℓ	
II-E Phytoplankton	Total zinc (particulate)	Zinc in phytoplankton in Monterey Bay, Calif.:	Knauer and Martin, 1973
		Period of intense upwelling = 100 μg/(g dry weight)	
		Period of low upwelling = 100-150 μg/(g dry weight)	
		Period of oceanic dominance = 300 μg/(g dry weight)	
II-F Detritus-microbial decomposers	Total zinc Pugettia producta	Concentration in fecal materials produced by herbivorous crab: 78 ± 28 μg (g ash weight)$^{-1}$	Boothe and Knauer, 1972
Arrow No. 33d (II-F, II-B)	Total zinc Pugettia producta	Deposition by marine bacteria: 85% of ^{65}zn removed from solution by bacteria within 120 hr	McLerran and Holmes, 1974
		20% sedimented with cells 80% sedimented by zn S or Fe S coprecipitate	
II-H Detritivores	Total zinc	Concentrations of zinc in detritivores from Great Sippewissett Salt Marsh, Mass.	Valiela et al., 1974
	Mercenaria mercenaria (clam)	Control 252 ± 9.7 ppm LF 296 ± 12.6 ppm HF 298 ± 20.0 ppm	
	Crassostrea virginica (oysters)	Control 12,675 ± 1,609 LF 9,650 ± 3,188 HF 7,650 ± 1,609	
Arrow No. 29 (II-H, II-D)	Soluble zinc	Zinc excretion by palaemon serratus (prawn)-- time required	Small et al., 1974
	Ionic particulate zinc	1-3 hr	
	Complexed zinc	4-5 hr	

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Table A20

Cycling of Cadmium in Marsh-Estuarine Ecosystems as Described by the Marsh-Estuarine Model

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
I-A Marsh soil	Total cadmium	Mean cadmium contents in top 2 cm of marsh soil:	Banus et al., 1975
		1.1 mg/m^2 (1971) 1.9 mg/m^2 (1972) Great Sippewissett Salt Marsh, Mass.	
		Mean cadmium contents in top 2 cm of marsh soil treated with low levels of fertilizer:	
		2.1 mg/m^2 (1971) 14.3 mg/m^2 (1972)	
		Mean cadmium contents in top 2 cm of marsh soil treated with high levels of fertilizer:	
		2.6 mg/m^2 (1971) 15.7 mg/m^2 (1972)	
		Average cadmium concentrations in marsh soils from southeastern salt marsh-estuaries in μg/(g dry weight of sediment) upper 40 cm:	Dunstan and Windom, 1975
		3.56 Santee River 0.79 Cooper River 0.69 Savannah River 1.2 Altamaha River 1.0 Satilla River 0.56 St. Johns River Average concentration = 1.19	
	Acid soluble cadmium	Concentration in top 2 cm of cores from fertilized plots	Valiela et al., 1974
		Control 1.7 mg/m^2 LF 13.4 mg/m^2 HF 11.8 mg/m^2	
I-B Marsh grasses	Total cadmium Spartina alterniflora	Mean concentration of cadmium in plants from Great Sippewissett marsh:	Banus et al., 1975
	Live plants	Control 1971 0.23 ± 0.03 ppm 1972 0.06 ± 0.01 ppm LF 1971 0.35 ± 0.05 ppm 1972 0.17 ± 0.05 ppm HF 1971 0.70 ± 0.08 ppm 1972 0.44 ± 0.06 ppm	
	Dead plants	Control 1972 0.14 ± 0.03 ppm HF 1972 0.92 ± 0.03 ppm	
	Spartina patens Live only	Control 1971 0.20 ± 0.04 ppm 1972 0.04 ± 0.04 ppm LF 1971 0.34 ± 0.03 ppm 1972 0.14 ± 0.03 ppm HF 1971 0.64 ± 0.12 ppm 1972 0.43 ± 0.08 ppm	
	Total cadmium	Average cadmium concentrations in plants from southeastern salt marsh-estuaries in μg/(g dry weight of sediment)	Dunstan and Windom, 1975
		0.85 Santee River 0.60 Cooper River 0.49 Savannah River 0.73 Altamaha River 0.58 Satilla River 0.38 St. Johns River Average = 0.61 (highly concentrated)	
I-E Detritus-microbial decomposers	Acid soluble cadmium	Concentration in acid soluble fraction of detritus	Valiela et al., 1974
		Control 1.15 ± 0.39 ppm LP 3.73 ± 0.94 ppm HF 5.50 ± 0.69 ppm	

(Continued)

Note: LF--from areas treated with low levels of fertilizer. HF--from areas treated with high levels of fertilizer.

(Sheet 1 of 3)

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Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
I-E Detritus-microbial decomposers (Continued)	Total cadmium *Rhizophora mangle*	Detritus from red mangrove leaves-- green leaf contents (μg/g dry weight): 0.33 ± 0.12 Barron River 0.24 ± 0.05 Shark River 0.19 ± 0.06 Broad River Cadmium content of leaves, litter, and detritus from Shark River and Broad River (μg/g dry weight):	Mathis, 1973

			Shark River	Broad River
	Green leaves		0.24 ± 0.05	0.19 ± 0.06
	Yellow leaves		0.26 ± 0.11	0.25 ± 0.16
	Litter		0.24 ± 0.04	0.29 ± 0.06
	Detritus		1.70 ± 0.89	0.97 ± 0.24

Comparative metal contents of suspended detritus (μg/g dry weight):

6.2 ± 5.7 Barron River
1.0 ± 0.2 Broad River
1.7 ± 0.9 Sharkey River

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
I-F Marsh detritivores	Total cadmium	Concentration of cadmium in marsh detritivores (ppm):	Banus et al., 1975
	Modiolus demissus (Ribbed Mussel)	Control 2.0 ± 0.3 ppm LF 3.0 ± 0.5 ppm HF 6.7 ± 2.2 ppm	
	Uca pugnax	Control 0.6 ± 0.2 ppm LF 0.5 ± 0.1 ppm HF 1.4 ± 0.6 ppm	
	Modiolus demissus	Control 1.98 ± 0.09 ppm LF 3.75 ± 0.13 ppm HF 7.15 ± 3.24 ppm	Valiela et al., 1974
II-B Estuarine sediment	Total cadmium	Total concentration of cadmium in suspended sediments (ppm): Suspended estuarine sediment = 8.7 Suspended river sediment (Arrow No. 36 III, IIA) = 15.8	Dunstan and Windom, 1975
		Mean concentration in suspended load of headwaters and mouths of Florida estuaries:	Mathis, 1973

	Salinity %	Suspended Load (mg/ℓ)	Cd (μg/g dry weight)
		Headwaters	
Shark	0-9.6	4.5	1.7 ± 0.9
Broad	--	8.5	1.0 ± 0.2
		Mouth	
Shark	23-25	14.0	1.1 ± 0.1
Broad	--	16.5	1.4 ± 0.5

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
		Deposition of cadmium by marine bacteria in estuarine sediments: 70 percent removed from solution in 120 hr-- 85-90 percent of amount removed was by precipitation, either as CdS or FeS coprecipitates	McLerran and Holmes, 1974
	Methyl cadmium	Cd biologically methylated, but resulting compounds are water-unstable	Thayer, 1973
II-C Periphyton and rooted *macrophytes*	Total cadmium	Concentration of cadmium in plants:	Boothe and Knauer, 1972
	Macrocystis pyrifera	3.4 ± 0.4 ppm	

(Continued)

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
II-C Periphyton and rooted macrophytes (Continued)	Fucus vesiculosus Fucus senatus	3.01 ppm Aberystwyth, Scotland 2.43 ppm Nefya, Scotland 3.35 ppm Aberystwyth, Scotland 3.25 ppm Nefya, Scotland	Fuge and James, 1973
II-D Dissolved mineral pool	Total cadmium	Total cadmium concentration in estuarine waters: 1.13 μg/ℓ in estuarine water of south-eastern estuaries 0.84 μg/ℓ in river waters feeding south-eastern estuaries	Dunstan and Windom, 1975
		Average concentrations in Monterey Bay, California:	Knauer and Martin, 1973
		Period of intense upwelling = 0.30 μg/ℓ Period of low upwelling = 0.11 μg/ℓ Period of oceanic dominance = 0.03 μg/ℓ Period of mixing = 0.09 μg/ℓ Concentration in surface waters of Pacific Ocean, Hawaii to Monterey = 0.02 μg/ℓ	
	Dissolved and particulate concentrations of cadmium	Concentrations in Florida estuaries:	Mathis, 1973

Barron River Station	Salinity %	Concentration of Cadmium (μg/g dry weight) Dissolved	Particulate
161	0	--	3.1
160	0	0.0009	2.8
157	2.5	0.0036	13.0

Shark River Station	Salinity %	Concentration of Cadmium (μg/g dry weight) Dissolved	Particulate
--	0	0.0003	0.9
--	5.5	0.0005	2.6
--	9.6	0.0005	1.6

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
II-E Phytoplankton	Total cadmium	Average concentrations of phytoplankton in Monterey Bay, California: Period of intense upwelling ≈ 1 μg/g dry weight Period of low upwelling = 1 μg/g dry weight Period of oceanic dominance ≈ 4 μg/g dry weight Period of mixing - not assessed Average surface water concentration	Knauer and Martin, 1973
II-F Detritus-microbial decomposers	Total cadmium	Cadmium content of herbivorous crab feces: 3.2 μg/g ash weight	Boothe and Knauer, 1972
		Cadmium content of suspended detritus from three Florida estuaries:	Mathis, 1973
		6.2 ± 5.7 μg/g dry weight - Barron River 1.0 ± 0.2 μg/g dry weight - Broad River 1.7 ± 0.9 μg/g dry weight - Sharkey River	
II-H Detritivores	Total cadmium	Cadmium contents of detritivores:	

	Mercenaria mercenaria (clams)	Control 1.25 ± 0.12 ppm dry weight LF 2.18 ± 0.13 ppm dry weight HF 2.08 ± 0.12 ppm dry weight	
	Crassostrea virginica (oysters)	Control 7.18 ± 0.52 ppm dry weight LF 8.60 ± 0.49 ppm dry weight HF 9.45 ± 0.51 ppm dry weight	Valiela et al., 1974
		Comparative cadmium uptake:	Eisler et al., 1972

	Concentration in mg/kg ash weight Active	Control
Fundulus heteroclitus (Mummichog)	52.1	9.3
Aquipecten irradians	82.7	43.0
Crassostrea virginica (oysters)	5.4	5.3
Homarus americanus (lobsters)	7.6	5.6

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Table A21

Cycling of Copper in Marsh-Estuarine Ecosystems as Described by the Marsh-Estuarine Model

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
I-A Marsh soil	Total copper	Average concentrations in soils of southeast salt marsh-estuaries in µg/g dry weight:	Dunstan and Windom, 1975

25.4	Santee River	
7.8	Cooper River	
14.7	Savannah River	
8.9	Altamaha River	
8.2	Satilla River	
2.7	St. Johns River	

Average concentration--11.4

Concentration in Danish intertidal area: Hallberg, 1974

Layer A	5.12 ppm
Layer B	1.38 ppm
Layer C	2.55 ppm
Layer D	0.43 ppm

Dissolved copper

Percent complexed in upland New York soils = 88.5 (7.99 ppb)   Hodgson et al., 1965

Percent complexed in calcareous soils = 98.9 (10.8 ppb)   Hodgson et al., 1966

Fractionation of copper in soil solution   Gerring and Hodgson, 1969

Fraction	Cu Complexed, %
Original soil solution	96
Concentrated soil solution	97
Concentrated nondialyzable soil solution	97
Concentrated dialyzable soil solution	90

Ratio of metal: ligand for soil solution complexes = 1.1

I-B Marsh grasses   Total copper

Average concentrations in marsh grasses from Southeast Salt Marsh-Estuaries: concentration in µg/g dry weight   Dunstan and Windom, 1975

Spartina alterniflora

3.95	Santee River
4.1	Cooper River
4.8	Savannah River
4.8	Altamaha River
3.8	Satilla River
1.67	St. Johns River

Average concentration = 3.9

Average contents in green leaves of red mangrove from Florida estuaries in µg/g dry weight   Mathis, 1973

Rhizophora mangle

2.2 ± 1.0	Barron River
0.9 ± 0.3	Shark River
1.6 ± 0.6	Broad River

I-E Detritus-microbial decomposer   Total copper

Average contents of mangrove leaves in various ages of decomposition in µg/g dry weight: Mathis, 1973

	Shark River	Broad River
Green leaves	0.9 ± 0.3	1.6 ± 0.6
Yellow leaves	0.6 ± 0.4	0.6 ± 0.4
Litter	1.3 ± 0.5	1.4 ± 0.4
Detritus	12.0 ± 4.0	8.0 ± 2.8

II-B Estuarine sediment   Total copper

Average concentration in suspended sediment in southeastern estuaries:

Estuarine sediment	58 µg/g dry weight
Riverine sediment	79 µg/g dry weight

Concentrations in suspended load of Florida estuaries   Mathis, 1973

(Continued)

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Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage				Reference

		River	Salinity percent	Suspended Load, mg/l	Concentrated Cu, µg/g dry Weight	
				Headwaters		
		Shark	0-9.6	4.5	12.0 ± 3.9	
		Broad	--	8.5	4.9 ± 1.5	
				Mouth		
		Shark	23-25	14.05	5.2 ± 0.0	
		Broad	--	16.5	5.6 ± 1.7	

Comparative value for fresh water

        Ottawa River   28 µg/g dry weight
        Rideau River   24 µg/g dry weight

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
II-C Periphyton and rooted macrophytes	Total copper	Contents of brown algae	Boothe and Knauer, 1972
	Macrocystis pyrifera	6.9 ± 2.7 µg/g ash weight	
	Fucus serratus	3.88 µg/g dry weight, Aberystwygh, Scotland 4.19 µg/g dry weight, Nefya, Scotland	
	Fucus vesiculosis	3.74 µg/g dry weight, Aberystwygh, Scotland 4.34 µg/g dry weight, Nefya, Scotland	

II-D Dissolved mineral pool	Soluble copper	Concentration in Southeastern Salt Marsh-Estuaries:
		
		    Estuarine water 3.3 ppb
		    Riverine water 4.5 ppb
			Dunstan and Windom, 1975

		Concentrations in Monterey Bay, Calif.: Period of intense upwelling = 1.7 µg/l Period of low upwelling = 1.0 µg/l Period of oceanic dominance = 1.1 µg/l Period of mixing = 1.5 µg/l Average Pacific Ocean surface water concentration, Hawaii to Monterey = 0.8 µg/l	Knauer and Martin, 1973

	Dissolved and particulate copper	Sample Stations	Salinity percent	Concentrated Cu in µg/l		Mathis, 1973
				Dissolved	Particulate	
		Barron River No.				
		161	0	--	0.32	
		160	0	0.0049	41.0	
		157	2.5	0.0071	120.0	
		Shark River No.				
		310	0	0.0010	12	
		309	5.5	0.0011	17	
		311	5.0	0.0008	8.6	

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
II-E Phytoplankton	Total copper	Average concentrations in phytoplankton in Monterey Bay, Calif.: Period of intense upwelling = 25 µg/g dry weight Period of low upwelling = 10 µg/g dry weight Period of oceanic dominance = 25 µg/g dry weight Period of mixing = not assessed	Knauer and Martin, 1973
II-F Detritus-microbial decomposers	Total copper *Pugettia producta*	Fecal material of herbivorous crab: 30 ± 1.8 µg/g ash weight	Boothe and Knauer, 1972

		Suspended detritus in Florida Estuaries:
		
		    Barron River 64 ± 49 µg/g dry weight
		    Broad River 49 ± 1.5 µg/g dry weight
		    Shark River 27 ± 3.2 µg/g dry weight
			Mathis, 1973

Table A22

Cycling of Mercury in Marsh-Estuarine Ecosystems as Described by the Marsh-Estuarine Model

Compartment No. and Name; Arrow No.	Form and Source of Mineral	Rate of Transfer or Amount of Storage	Reference
I-A Marsh soils	Total mercury	Average concentrations in soils of Southeast salt marsh-estuaries in µg/g dry weight: 0.09 Santee River 0.03 Cooper River 0.11 Savannah River 0.10 Altamaha River 0.07 Satilla River 0.04 St. Johns River Average concentration = 0.08	Dunstan and Windom, 1975
II-B Marsh grasses	Total mercury in *Spartina alterniflora*	Average concentrations in plants of Southeast Salt Marsh-Estuaries in µg/g dry weight: 0.17 Santee River 0.5 Cooper River 0.44 Savannah River 0.27 Altamaha River 0.27 Satilla River 0.25 St. Johns River Average concentration = 0.32 (highly concentrated from marsh soil)	Dunstan and Windom, 1975
Arrow No. 1 (I-A, I-B)	Organic and inorganic mercury *Spartina alterniflora*	Uptake and transfer in marsh grasses: 20-25% of available mercury taken up by roots at equilibrium. Estimated total uptake of mercury by *Spartina* = 0.7 mg:m^2:yr with at least 35 µg:m^2:yr (5%) of this amount taken up and released to the water (forms studied were CH_3HgCl and $HgCl_2$)	Rahn, 1973
II-B Estuarine sediments	Total mercury	Concentration in suspended sediments in Southeast Salt Marsh-Estuaries: Estuarine sediment = 0.86 ppm Riverine sediment = 0.81 ppm	Dunston and Windom, 1975
		Comparative freshwater values: Ottawa River = 0.28 ppm Rideau River = 0.20 ppm	Oliver, 1973
		Concentration in Puget Sound, Wash.: Near Chlor-Alkalai Plant = 0.01-0.5 ppm Other areas = 0.01-0.1 ppm	Crecelius et al., 1975
		82% of materials in sediments associated with easily oxidizable organic matter	
II-B Estuarine sediments and Arrow No. 17 (II-B, II-D)	Inorganic and methyl mercury	Activities mobilizing mercury	
		Methylation of mercury:	Thayer, 1973
		Mercury release for bottom sediments and rotten fish	Jensens and Jernelöv, 1969
		440 ng CH_3Hg^+ released in 10 days from 100 ppm $HgCl_2$/g bottom sediments	
		40 ng CH_3Hg^+ released in 10 days from 100 ppm CH_3HgCl/g bottom sediments	
		10 µg $(CH_3)_2Hg$ released in 4 days from mixture of 5 g of *Xiphophorus helleni*, 10 g of *Gadus colja*, and 60 µg $HgCl_2$	
		Metabolism of mercury	Matsumara et al., 1971
		3.23 mg total Hg/kg sediment/day in natural sediments	Jernelöv et al., 1975 Jernelöv, 1970
II-D Dissolved mineral pool	Dissolved mercury	Concentration in waters in Southeast Salt Marsh-Estuaries: Estuarine waters	
		Estuarine water--none found River water = 0.07 ppb Georgia estuaries = 1.5 mg/m^2/yr	Dunstan and Windom, 1975 Rahn, 1973
II-E Phytoplankton	Total mercury	Offshore diatoms: 181 ± 50 ng Hg/g dry weight Oregon coast: 446 ng Hg/g dry weight Monterey Bay, Calif.: 8.4 ng Hg/g dry weight	Knauer and Martin, 1973
II-G Herbivores	Total mercury	Offshore zooplankton: 145 ± 14 ng Hg/g dry weight Oregon coast zooplankton: 23 ng Hg/g dry weight Miscellaneous fishes: Average of four mesopelagic fishes = 40 ng/g wet weight Monterey Bay anchovy = 53 ng/g dry weight	Knauer and Martin, 1973

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